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# *A STUDY OF 7900 EXTERNAL GALAXIES*

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1. The general survey of faint galaxies; based on long exposure photographs with the Bruce and Metcalf doublets at the South African and Oak Ridge stations of the Harvard Observatory, has to date yielded something over 150,000 new objects. More than a third of the sky has been covered. The survey is essentially complete to photographic magnitude 17.5, and tens of thousands of fainter objects are included; the faintest objects approximate magnitude 18.5.

The current program includes completion of the photographs for the whole sky, repetition of low quality plates, search for and marking of all nebulae to the limits of the plates, and the measurement of photographic magnitudes, using stellar sequences determined, for the most part, by the star count method. The plan includes also a detailed study of the individual nebulae in conspicuous clusters of galaxies and in a few typical areas in order that through the analysis of these large samples we can gain, for faint nebulae in general, a fair idea of the frequency distributions in angular diameter, magnitude, form and structural detail.

The present communication reports on the third and largest of the detailed studies. The first was published in 1930 by Miss Ames, who cataloged 2778 objects in the northern galactic hemisphere in the constellations of Coma and Virgo.[1] The second was published two years ago by Professor R. H. Baker of the University of Illinois, and dealt with 985 objects in Eridanus in the southern galactic hemisphere.[2] The region of the present survey covers 174 square degrees of the southern galactic hemisphere in the constellations Dorado, Horologium and Reticulum. A fourth detailed analysis, in the hands of Mr. Carl Seyfert, will include a strip of nine fields in galactic longitude 110°, extending from near the north galactic pole to the galactic equator.

2. Twelve long exposure photographs made at the southern station with the Bruce refractor (1 mm. = 1′) are used in the present exploration; in addition, several plates of smaller scale provide more suitable images

for the determination of magnitudes of the larger and brighter galaxies. Details of the plates and the methods of measurement appear, along with the catalog of galaxies, in the Annals of the Harvard Observatory, Volume 88, No. 5. Miss S. F. Mussells has been responsible for the major part of the measuring and reductions.

The area covered lies between galactic longitudes 215° and 245°, and latitudes −38° and −59°. It is sufficiently remote from the galactic circle

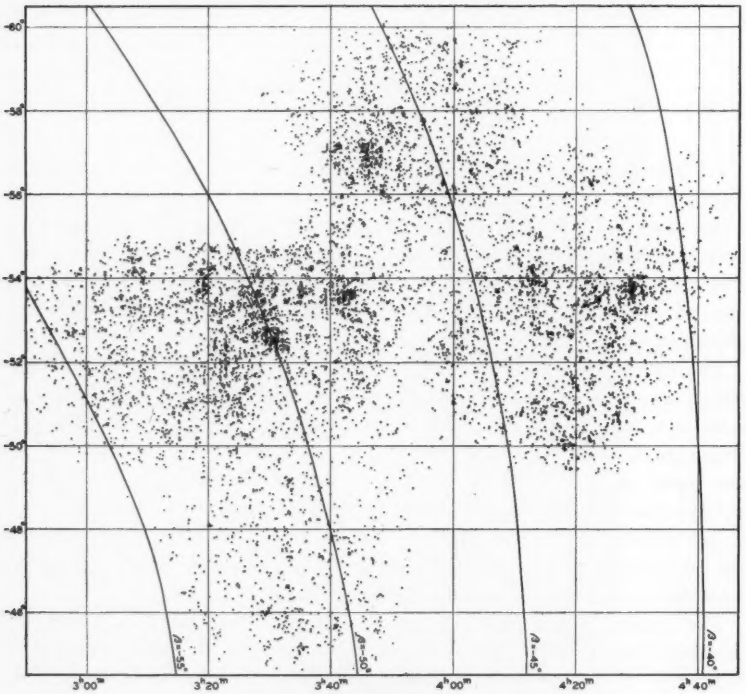


FIGURE 1

The distribution of the galaxies.

to be free from obscuration by outlying streamers from the Milky Way. The distribution of the 7900* galaxies on the surface of the sky is shown in figure 1, which illustrates: (*a*) a considerable departure from uniform distribution; (*b*) the presence of several fairly distinct groupings; (*c*) the apparent failure, near the edges of the plates, to record the faintest galaxies. The plate-edge deficiency leads us to segregate for discussion the areas within 2°.5 of the plate center.

In the region under study, only 134 objects were known previously (less

than two per cent of the present total), and all but twenty-five of these were found some years ago on early Harvard plates. A few bright spirals are in the region, but for none of them has the velocity been determined; in none have individual stars been detected.

3. An examination of the distribution of apparent magnitudes, as shown in tables 1 and 2 and in the frequency curves of figure 2, reveals for this large region greater deviation than usual from average space density. The broken line indicates the frequency that would be expected for uniform density and average richness. Its scale of ordinates, on the left of the figure, is the same as that for the general field (exclusive of clusters); that is, the full curve with dots and the uniform density curve refer to the same amount

TABLE I

MAGNITUDE-DIAMETER DISTRIBUTION IN CENTRAL AREAS

| D\m | 15.0 | 15.1 | 15.6 | 16.1 | 16.6 | 17.1 | 17.6 | 18.1 | TOTAL |
|---|---|---|---|---|---|---|---|---|---|
| 6′ | | | | | | 1 | 1 | | 2 |
| 12 | | | | 18 | 108 | 232 | 169 | 6 | 533 |
| 18 | | 1 | 19 | 83 | 332 | 829 | 557 | 84 | 1905 |
| 24 | | 3 | 17 | 128 | 433 | 723 | 529 | 104 | 1937 |
| 30 | | 4 | 9 | 71 | 141 | 190 | 129 | 26 | 570 |
| 36 | 1 | 4 | 5 | 34 | 81 | 77 | 31 | 11 | 244 |
| 42 | | 1 | 7 | 20 | 35 | 31 | 6 | 3 | 103 |
| 48 | 3 | 2 | 4 | 6 | 16 | 11 | 3 | 1 | 46 |
| 54 | | 1 | 4 | 9 | 9 | 1 | 4 | | 28 |
| 60 | 2 | | 3 | 1 | 4 | 4 | | | 14 |
| 66 | | 3 | 2 | 8 | 3 | 1 | | | 17 |
| 72 | 1 | | 2 | 2 | 4 | 2 | | | 11 |
| 78 | | 1 | | 1 | 1 | | 1 | | 4 |
| 84 | 1 | 1 | 1 | 2 | 2 | | | | 7 |
| 90 | | | | 2 | 1 | | | | 3 |
| 96 | 1 | 1 | | 1 | | | | | 3 |
| 102 | | | | 2 | 1 | | | | 3 |
| >102 | 17 | 1 | 2 | | 1 | | | | 21 |
| Total | 26 | 23 | 75 | 388 | 1172 | 2102 | 1430 | 235 | 5451 |

of the sky (115 square degrees). From the figure it is clear that even outside the clusters the number of galaxies per square degree in the Horologium region is approximately twice the average that has been found in Harvard and Mount Wilson studies. Also, it appears from the sudden increase in number of galaxies for photographic magnitudes between 15.5 and 17.0 that the superabundance of objects in this direction is due to the presence of a metagalactic cloud, with a maximum in its luminosity curve between magnitudes 17.0 and 17.5. The deduced distance of the cloud, if these are normal systems, is of the order of twenty-two megaparsecs.

Grouping the material for the five observed clusters into a single luminosity curve (full line with crosses), we infer that their distances are much

the same as that of the general metagalactic cloud. In an earlier study their distances, on the average, were found to be twenty-five megaparsecs.[3] In fact, it is probable that these clusterings are merely aggregations in the more comprehensive system; they are, for example, not as distinct as the cluster in Coma.[4] The deficit in the number of galaxies from magnitude 14.5 to 15.5, compared with the average for the sky, is not of particular significance because the numbers involved are small and irregularities in distribution to the fifteenth magnitude are found everywhere.

The question may be raised as to whether the evidence for a metagalactic cloud noted above may not be attributable to error in the magnitude scale. Such an explanation is unacceptable because the abnormality in question is found consistently throughout the area, and when exactly the same method here employed is used also in other parts of the southern

TABLE 2

MAGNITUDE-DIAMETER DISTRIBUTION IN CLUSTERS

| D\m | 15.0 | 15.1 | 15.6 | 16.1 | 16.6 | 17.1 | 17.6 | 18.1 | TOTAL |
|---|---|---|---|---|---|---|---|---|---|
| 6″ | | | | | | 1 | | | 1 |
| 12 | | | | 2 | 2 | 17 | 26 | 6 | 53 |
| 18 | | | | 12 | 73 | 193 | 194 | 22 | 494 |
| 24 | | 1 | 4 | 14 | 107 | 217 | 198 | 23 | 564 |
| 30 | | 1 | | 14 | 30 | 44 | 34 | 3 | 126 |
| 36 | | | | 8 | 7 | 13 | 7 | 1 | 36 |
| 42 | | | | 5 | 8 | 1 | 4 | | 18 |
| 48 | | | | 4 | 4 | 3 | 1 | | 12 |
| 54 | | | | | | 1 | 1 | | 2 |
| 60 | | | | | 2 | | | | 2 |
| 66 | | | 1 | 1 | 1 | 2 | | | 5 |
| 72 | | | | 2 | | 1 | | | 3 |
| >72 | 2 | | | 2 | 1 | 1 | | | 6 |
| Total | 2 | 2 | 5 | 64 | 235 | 494 | 465 | 55 | 1322 |

sky the results agree with prediction from the hypothesis of uniformity. It is probable that this large irregular system of galaxies which appears to be centered in Horologium will be found upon the completion of the "eighteenth magnitude survey" to extend throughout several of the surrounding constellations.

4. The distribution of diameters, as measured to the tenth of a minute of arc on the Bruce photographs with superposed millimeter scale, is also illustrated in tables 1 and 2. Ninety per cent of all the nebulae have diameters of 0′.2 to 0′.5. In comparison with the general field (central areas) the proportion of objects in the clusters with angular diameters greater than 1′.2 is low.

The considerable spread in the tabulated quantities of table 2 is a reflection of the real dispersion in the true values of angular diameters and apparent magnitudes, since the measuring errors are of the order of only

two seconds of arc and eight hundredths of a magnitude. The complete frequency curves of dimensions and absolute magnitudes are of course not attainable from the present material; in both the metagalactic cloud and its involved clusters of galaxies a large part of the population is undoubtedly below the faintest limit of the plates.

5. In the mean, the measurable size of a galaxy decreases with bright-

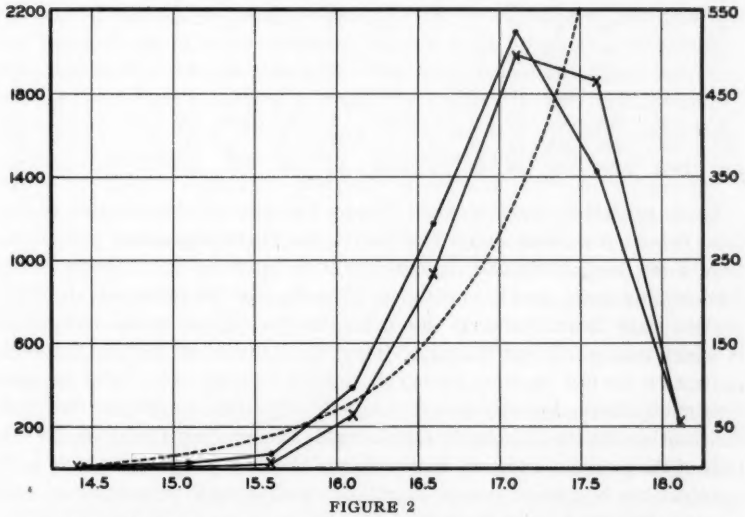


FIGURE 2

Frequency of magnitudes. Dots, with scale on left, refer to numbers of nebulae in all central areas exclusive, however, of the five regions of clusters of galaxies. Crosses, with scale on right, refer to the regions of clusters. The broken line represents the hypothesis of uniform distribution in space (see text).

ness; the correlation coefficient between apparent magnitude and angular diameter and its standard deviation is as follows:

| | Central Areas | Clusters |
|---|---|---|
| $r$ | −0.277 | −0.272 |
| $\sigma$ | 0.014 | 0.026 |

The strong significance of the correlation, especially in the clusters where differences in distance may be most safely assumed to be unimportant, shows that in these congested regions (one galaxy to $5 \times 10^{15}$ cubic light-years) there is a genuine correlation between intrinsic brightness and measured *linear* size. Perhaps some of this relation should be attributed to photographic failure to record the outer part of the fainter nebulae.

TABLE 3

FREQUENCY OF CLASSES

| FORM | CENTRAL AREAS CONCENTRATION | | | | | | ALL | FORM | CLUSTERS CONCENTRATION | | | | | | ALL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *a* | *b* | *c* | *d* | *e* | *f* | | | *a* | *b* | *c* | *d* | *e* | *f* | |
| 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 1 | 3 | 3 | 0 | 0 | 7 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 2 |
| 3 | 1 | 8 | 4 | 2 | 3 | 1 | 19 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 2 |
| 4 | 8 | 13 | 11 | 8 | 1 | 2 | 43 | 4 | 1 | 3 | 1 | 1 | 2 | 5 | 13 |
| 5 | 33 | 49 | 41 | 8 | 6 | 6 | 143 | 5 | 3 | 3 | 9 | 7 | 4 | 1 | 27 |
| 6 | 70 | 87 | 65 | 7 | 4 | 0 | 233 | 6 | 9 | 15 | 15 | 4 | 1 | 2 | 46 |
| 7 | 199 | 242 | 83 | 6 | 2 | 1 | 533 | 7 | 33 | 40 | 47 | 3 | 1 | 0 | 124 |
| 8 | 549 | 611 | 198 | 10 | 5 | 3 | 1376 | 8 | 78 | 127 | 98 | 7 | 1 | 1 | 312 |
| 9 | 764 | 934 | 307 | 22 | 7 | 7 | 2041 | 9 | 117 | 216 | 126 | 6 | 0 | 1 | 466 |
| 10 | 320 | 491 | 218 | 12 | 4 | 9 | 1054 | 10 | 46 | 146 | 131 | 4 | 2 | 1 | 330 |
| All | 1944 | 2436 | 931 | 79 | 32 | 29 | 5451 | All | 287 | 551 | 428 | 32 | 13 | 11 | 1322 |

6. A general discussion of the "Bruce" system of classification of the faint nebulae,[5] with an analysis of the relations between central concentration, form, magnitude and diameter, will be made by Mr. Seyfert in his forthcoming study, mentioned above. The distribution of objects throughout the sixty Bruce classes is shown for the Horologium region in table 3, in which it is noted that the classes (*d*, *e* and *f*) involving high central concentration are not common among these faint objects. The forms are predominately in the low elongation groups 7 to 10, with practically the same distribution for the clusters as for the fields surrounding them. In all details of the present study we find evidence that the clusters are only rich aggregations in a large system of galaxies with a total population of well over ten thousand individuals.

* Actually 7889, since eleven were dropped as duplicates in the course of preparing the catalog for the press; some of the tabulations here described are based on 7900 observations.

[1] *Harv. Ann.*, **88**, No. 1 (1930).

[2] *Harv. Ann.*, **88**, No. 3 (1933).

[3] These PROCEEDINGS, **19**, 1001 (1933).

[4] Hubble and Humason, *Mt. W. Contr.* 427 (1931); Shapley, *Harv. Bull.*, 896 (1934).

[5] Shapley, *Harv. Bull.*, 849 (1927); A. Ames, *Harv. Ann.*, **88**, No. 1 (1930).

# THE ANGULAR DIAMETERS OF GLOBULAR CLUSTERS

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1. The values of the angular diameters of globular clusters which have been used in estimating relative distances and average linear dimensions[1] were based on direct visual measures with a scale on photographs made with cameras of various focal lengths. The measures admittedly do not encompass the outlying stars, and in fact refer chiefly to the central region of each system. For a globular cluster the definition of diameter, apparent or linear, is necessarily vague. Since the stellar distribution is such that there is no definite boundary, estimates of diameter vary with telescope, exposure time and the observer's convention in making the measures. Hertzsprung has suggested the description of dimensions in terms of the central area that includes a fixed proportion (say one half) of the total light of the cluster. But the practical difficulties in measuring a cluster's total light, and especially in measuring the distribution of luminosity throughout a globular cluster, stand in the way, as yet, of a general use of Hertzsprung's convention.

For the comparative study of globular clusters it seems worth while to make the decided improvement on previous estimates of diameters that is now possible through the use of densitometer tracings based on a fairly homogeneous series of negatives. We have selected photographs in the *B*, *MF*, *RB* and *RH* series (ranging in scale from 1 mm. = 390″ to 1 mm. = 167″) for sixty-four of the known globular clusters of the galactic system; three plates taken with the 16-inch Metcalf doublet (1 mm. = 98″) and three taken with the Bruce telescope (1 mm. = 60″) are used for clusters that are not suitably photographed in the other series. Tracings of the seventy clusters were made with the Moll densitometer, with a magnification over the original negative of 5.4.

2. The angular diameters, measured generally in two position angles, are given in the accompanying table. The class of each globular cluster is taken from the tables in Harvard Observatory Monograph No. 2, with a revision for N. G. C. 4147 suggested by Dr. Baade. In the last column are given the ratios of the new measures to those previously published.[1] The mean ratio is 3.7 ± 0.14 (p. e.), all the clusters now being measured larger than before, and seventy per cent between twice and five times as large.

The differences between the two values tabulated for each cluster are an indication of the uncertainty of measurement with the densitometer rather than a measure of elliptical form. The average deviation of a single measure from the corresponding mean value is 4.8 per cent, with only

six deviations greater than ten per cent. Elliptical forms have previously been found for many of these clusters by the direct measures that dealt chiefly with the inner part of the cluster structures. That the denser central regions may exhibit distinct oblateness—a circumstance that is fully verified by star counts[2]—while at greater distances from the center, where star population is sparse, the oblateness does not appear, is probably of considerable interest in the dynamics of globular clusters. An analogy appears in the star distribution in the Andromeda Nebula,[3] and possibly in the distribution of faint cluster type Cepheids in the galactic system. Although the oblateness of $\omega$ Centauri is not shown by the densitometer measures of total diameter, the tracings do clearly indicate the elliptical distribution of total brightness in the main body of the cluster. With appropriately calibrated plates it will be simple to make an iso-photo map of the system.

DIAMETERS OF GLOBULAR CLUSTERS

| N. G. C. | PLATE SERIES | EXPOSURE m | CLASS | DIAMETER N–S | DIAMETER E–W | MEAN | RATIO NEW/H.MON.2 |
|---|---|---|---|---|---|---|---|
| 104 | MF | 60 | III | 60′.5 | 52′.6 | 56′.5 | 2.4 |
| 104 | RB | 90 | III | 49.2 | 52.2 | 50.7 | 2.2 |
| 288 | B | 60 | X | 12.8 | 13.4 | 13.1 | 1.3 |
| 362 | MF | 60 | III | .. | 17.7 | .. | 3.3 |
| 1851 | MF | 60 | II | 11.5 | .. | .. | 2.2 |
| 1904 | RB | 90 | V | 10.3 | 8.5 | 9.4 | 2.9 |
| 2298 | B | 60 | VI | 3.7 | 4.2 | 3.9 | 2.2 |
| 2419 | MC | 45 | VII | .. | .. | 5.1 | 3.0 |
| 2808 | MF | 60 | I | 19.3 | 18.2 | 18.8 | 3.0 |
| 3201 | RB | 90 | X | 28.9 | 29.6 | 29.3 | 3.8 |
| 4147 | MC | 40 | III | 2.9 | 2.7 | 2.8 | 1.6 |
| 4372 | B | 65 | XII | 20.6 | 19.1 | 19.8 | 1.6 |
| 4833 | B | 60 | VIII | 13.1 | 12.3 | 12.7 | 2.7 |
| 5024 | RH | 67 | V | 16.6 | 15.1 | 15.8 | 4.8 |
| 5139 | RB | 90 | VIII | 65.6 | 65.2 | 65.4 | 2.8 |
| 5272 | RB | 70 | VI | .. | .. | 22.1 | 2.2 |
| 5286 | B | 62 | V | 13.7 | 13.4 | 13.6 | 8.5 |
| 5634 | MF | 45 | IV | 6.8 | .. | .. | 5.2 |
| 5824 | B | 60 | I | 9.7 | 10.6 | 10.2 | 10.2 |
| 5897 | RB, B | 90, 60 | XI | 13.4 | 12.9 | 13.1 | 1.8 |
| 5904 | RB | 90 | V | 27.7 | 22.3 | 25.0 | 2.0 |
| 5927 | A | 60 | VIII | 11.5 | 12.5 | 12.0 | 4.0 |
| 5986 | B | 60 | VII | 8.7 | 7.8 | 8.2 | 2.2 |
| 6093 | MF | 45 | II | 13.0 | 15.6 | 14.3 | 4.3 |
| 6101 | RB | 90 | X | .. | .. | 14.6 | 3.8 |
| 6121 | MF | 45 | IX | 26.0 | 26.6 | 26.3 | 1.9: |
| 6144 | MF | 45 | XI | 10.4 | 10.9 | 10.6 | 3.2 |
| 6171 | B | 60 | X | 9.5 | 9.6 | 9.6 | 4.4 |
| 6205 | RH | 60 | V | .. | .. | 18.1 | 1.8 |
| 6218 | RB | 90 | IX | .. | 21.0 | .. | 2.3 |
| 6229 | MC | 39 | VII: | 5.0 | 5.6 | 5.3 | 4.4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 6235 | B | 60 | X | 9.3 | 8.9 | 9.1 | 4.8 |
| 6254 | RB | 90 | VII | 22.9 | 20.1 | 21.5 | 2.6 |
| 6266 | B | 62 | IV | 14.7 | 14.0 | 14.4 | 3.3 |
| 6273 | B | 62 | VIII | 14.5 | 14.5 | 14.5 | 3.4 |
| 6284 | B | 62 | IX: | 7.8 | 9.5 | 8.6 | 5.7 |
| 6287 | B | 60 | VII | 6.1 | 6.1 | 6.1 | 3.6 |
| 6293 | B | 62 | IV | 8.6 | 8.4 | 8.5 | 4.5 |
| 6304 | B | 62 | VI | 8.1 | 10.6 | 9.4 | 5.9 |
| 6316 | B | 62 | III | 6.4 | 6.1 | 6.2 | 5.6 |
| 6325 | MF | 45 | IV: | 5.2 | 5.7 | 5.4 | 7.7 |
| 6333 | MF | 45 | VIII | 12.5 | 12.0 | 12.2 | 5.1 |
| 6342 | MF | 45 | IV | 4.2 | 4.7 | 4.5 | 9.0 |
| 6352 | B | 65 | XI: | 9.5 | 8.4 | 8.9 | 3.6 |
| 6356 | MF | 45 | II | 10.9 | 9.9 | 10.4 | 6.1 |
| 6362 | A | 45 | X | 8.4 | 8.6 | 8.5 | 1.4 |
| 6388 | B | 60 | III | 7.8 | 10.3 | 9.0 | 2.6 |
| 6397 | RB | 90 | IX | 38.4 | 47.0 | 42.7 | 2.3 |
| 6402 | RB | 90 | VIII | 14.1 | .. | .. | 4.7 |
| 6441 | MF | 45 | III | 6.6 | .. | .. | 2.9 |
| 6453 | MF | 45 | IV | 3.6: | 3.6: | 3.6: | 5.1 |
| 6496 | B | 61 | XII | 13.1 | 12.3 | 12.7 | 5.8 |
| 6541 | RB | 90 | III | 21.9 | 24.4 | 23.2 | 3.7 |
| 6553 | B | 62 | XI | 6.2 | 7.0 | 6.6 | 3.9 |
| 6584 | MF | 45 | VIII | 9.9 | 9.4 | 9.7 | 3.9 |
| 6626 | B | 63 | IV | 15.1 | 14.8 | 15.0 | 3.2 |
| 6637 | B | 60 | V | 9.2 | 10.9 | 10.0 | 3.6 |
| 6638 | MF | 45 | VI | 4.7 | 5.0 | 4.8 | 3.4 |
| 6652 | B | 60 | VI: | 8.1 | 6.7 | 7.4 | 4.4 |
| 6656 | RB | 90 | VII | 39.4 | 29.9 | 34.7 | 2.0 |
| 6681 | B | 60 | V | 10.4 | 8.9 | 9.6 | 3.8 |
| 6715 | MF | 45 | III | 14.1 | 13.0 | 13.6 | 6.5 |
| 6723 | MF | 45 | VII | 12.2 | 11.7 | 12.0 | 2.1 |
| 6752 | RB | 90 | VI | 36.8 | 47.0 | 41.9 | 3.2 |
| 6779 | A | 30 | X | 7.1 | 7.4 | 7.2 | 4.0 |
| 6809 | RB | 90 | XI | 32.3 | 25.1 | 28.7 | 2.9 |
| 6864 | B | 73: | I | 8.4 | 9.0 | 8.7 | 4.6 |
| 6981 | B | 63 | IX | 8.4 | 7.6 | 8.0 | 4.0 |
| 7078 | RH | 60 | IV | 18.7 | 17.5 | 18.1 | 2.4 |
| 7089 | RB | 90 | II | 16.9 | 16.9 | 16.9 | 2.1 |
| 7099 | B | 60 | V | 10.9 | 10.5 | 10.7 | 1.9 |

3. The angular diameters of globular clusters are recognized as useful criteria of the distances. In figure 1 the new diameters are plotted against the values of the distances published in Harvard Observatory Monograph No. 2. These distances have not been corrected for space absorption in low galactic latitude; and until some way is devised to estimate the correction necessary for each individual beclouded cluster, the new diameters are valuable for the revision of distances only in the higher latitudes and in the regions of the Milky Way that are shown by the presence of external galaxies to be essentially clear of absorbing material.

If the Harvard distances are corrected for space absorption according to the formula of Stebbins[4] the correlation between distance and diameter is not satisfactory—a result that should be expected, since the formula was based on the untenable hypothesis of a thin homogeneous absorbing layer near the plane of the galaxy. A number of low latitude clusters show practically no absorption effect when tested by the color indices of their individual stars or by the integrated color excess as measured with Stebbins' photoelectric photometer; others in the same latitudes show conspicuous photoelectric color excess and a few are partially obscured by recognized

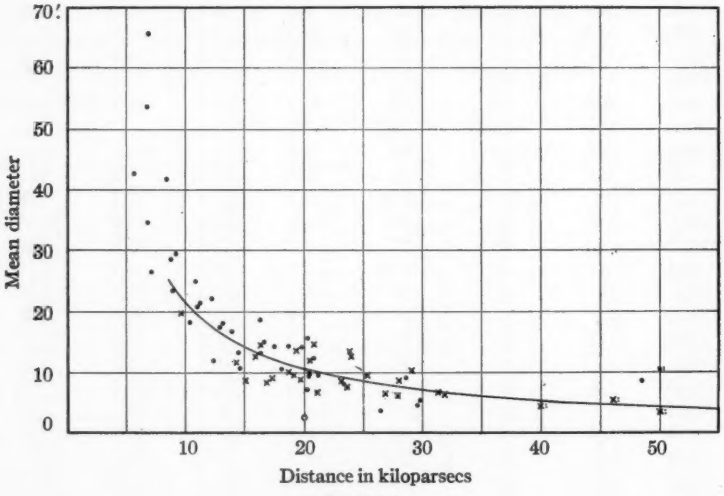


FIGURE 1

Relation, for seventy globular clusters, of diameters measured with densitometer to distances uncorrected for absorption. N. G. C. 2419 is off the diagram, with distance = 72.5, diameter = 5.1.

dark nebulosity. Many investigations have indicated the great unevenness of the absorption, both in longitude and in latitude, but it may be possible nevertheless to make corrections to the distances in low latitude when we have complete surveys of the external galaxies and much more material on color excesses and spectra for individual southern globular clusters.

The curve in figure 1 is computed from the relation $rD = 215$, where the distances, $r$, are given in kiloparsecs and the diameters, $D$, in minutes of arc. In deriving the constant, the high-latitude abnormal system N. G. C. 4147 has been ignored, as have also six clusters with uncorrected distances less than 8.5 kiloparsecs. For such near-by objects the diameter measures

are not comparable with measures of the fainter and more remote systems. The surprisingly small dispersion about the curve again emphasizes the general similarity in linear dimensions of the globular clusters of the galactic system. The plotted crosses refer to clusters whose computed distances involve only the earlier measures of diameter and integrated magnitudes; the distances for the others are based chiefly on magnitudes of bright stars and variables. The open circle represents N. G. C. 4147.

A study of the deviations from the mean curve of figure 1 shows no systematic relation of deviation to class of cluster or to galactic latitude. This lack of correlation with latitude is unexpected, in view of the effect on the measurement of distances that space absorption in low latitudes should produce. It may indicate that the angular diameters and the apparent total brightness are about equally undermeasured wherever the absorption is serious.

[1] H. Shapley and H. B. Sawyer, *Harv. Bull.* 852 (1927); Shapley, "Star Clusters," *Harv. Obs. Mon.*, No. **2** (1930).

[2] F. G. Pease and H. Shapley, *Mt. W. Contr.*, 129 (1917); O. Heckmann and H. Siedentopf, *Gött. Veröff.*, **6** (1929); *Zeit. Phys.*, **54**, 183 (1929).

[3] H. Shapley, *Darwin Lecture, M. N.*, **94**, 791 (1934); P. Vocca, *Mem. Soc. Astr. Ital.*, **9**, 1 (1935).

[4] These PROCEEDINGS, **19**, 222 (1933).

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## *INCREASED MUTATION RATE FROM AGED DATURA POLLEN*

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Since recent tests of aged seeds showed increased mutation rate, as indicated by pollen abortion,[2] together with parallel increase in the rate of visible recessive gene mutations in the same material,[3] it was thought possible that aging pollen might have similar effects. A rather limited series of experiments, using very simple methods of handling the material and making the tests, was accordingly undertaken. The results, however, were so positive, and the possible significance and applicability of the method so general, that it seemed best to describe the methods used and the results thus far obtained.

The plants used were grown from fresh seed of the Standard Line 1 of Datura. This line has been highly inbred, and has been passed through a haploid. It has been used in other mutation rate experiments, and as the standard in the general breeding work with Datura. Anthers were picked

just before they opened, and were placed on separate numbered slips of paper in a Syracuse dish. The pollen remained in the anther or on the paper beneath until used. A pollen sample from each flower was examined microscopically to see that it was normal in appearance. The uncovered dishes containing the pollen were stored in a cupboard which was heated by electric light bulbs connected to a thermostat. The thermometer in the cupboard registered 29 to 31°C. during the experiment, except that on one night the thermostat stuck and the temperature of the cupboard went down to about 18°C. Only two of the eight series of flowers were subjected to this change. The pollen was stored at about 30°C. in order to keep it somewhat above room temperature, and hence drier than it might otherwise have been. This temperature (about 85°F.) falls within the range of air temperatures to which flowers of Datura are normally subjected in the greenhouse and field. The pollen was shielded from the direct rays of the electric lamps. When pollinations were made, the dish with the pollen was carried to the greenhouse and the pollen there applied, either directly from the anther or from the paper slip, to the stigma of a previously emasculated flower. The flowers used as females were somewhat varied in age, but all were in good condition and neither extremely young nor extremely old. Crosses were attempted at intervals from two to twenty days after the pollen was stored. The distribution of the pollinations made and capsules set, in relation to the age of the pollen, is shown in table 1.

TABLE 1

| Age of pollen, days | 2–3 | 4–5 | 6–7 | 8–9 | 10–11 | 12–13 | 14–15 | 16–17 | 18–20 | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Pollinations made | 4 | 6 | 5 | 8 | 42 | 25 | 26 | 22 | 20 | 158 |
| Large capsules set | 2 | 2 | 0 | 3 | 1 | 4 | 0 | 0 | 0 | 12 |
| Small capsules set | 1 | 2 | 2 | 0 | 7 | 2 | 0 | 0 | 0 | 14 |

The use of pollen abortion as an index of the mutation rate has been discussed in an earlier paper[2] where the technique employed is described. Two types of abortion, due respectively to gene and to grosser chromosomal mutations, can be distinguished with a fair degree of accuracy by differences in appearance of the aborted grains. The classification of mutations in table 2 is based on this appearance of the grains and not on cytological study or breeding behavior. The highest rate of pollen abortion mutations found in our aged seed experiments was 8.7% for 21 mutations in 242 plants grown from seven- to eight-year old seed.[2] Experiments with heat and other factors (excepting strong radiation) have given lower rates from treated seeds. It seems clear, however, that higher rates have been induced by the use of aged pollen. A total of 29 pollen abortion mutations have been recorded in 193 plants from pollen aged for four to thirteen days, giving a mutation rate of 15.0%. The 191 control plants, grown from

the fresh seeds of a self (made with fresh pollen) on a sib of the plants used for the tests, showed no mutations. The data are shown in table 2. The mutation rates from progenies of fewer than five plants average very high, but the number of plants is extremely small. Percentages for these cases have been put in parentheses in table 2. From these small progenies there are 18 plants recorded with nine, or 50.0%, showing pollen abortion. The conditions of the storage of the pollen, especially in respect to moisture content, were not accurately controlled. It would appear that the conditions which adversely affected the size of the progenies tended to raise the mutation rate. Among the larger progenies, those from eight- to ten-day old pollen show higher rates of mutation than do those from five- to six-day old pollen. The rates are, respectively, 13.9% from 122 plants with 17 mutations, and 5.7% from 53 plants with three mutations.

TABLE 2

POLLEN ABORTION MUTATIONS FROM AGED POLLEN

| POLLEN AGE, IN DAYS | PARENT (341) NOS. | PROGENY NO. | SEEDS SOWN | PLANTS GROWN | PLANTS RECORDED | NORMALS | MUTATIONS | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | CHROMOSOMAL | GENE TYPE | TOTAL | PERCENTAGE |
| 4.00 | 93 × 37*A** | 3401821 | 8 | 3 | 2 | 1 | 1 | 0 | 1 | (50.0) |
| 5.00 | 60 × 71*A* | 3401822 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | (0.0) |
| 5.25 | 73 × 37*B* | 3401815 | 42 | 35 | 34 | 32 | 1 | 1 | 2 | 5.9 |
| 5.75 | 71 × 77*B* | 3401816 | 29 | 19 | 19 | 18 | 1 | 0 | 1 | 5.3 |
| 6.75 | 54 × 77*A* | 3401823 | 5 | 3 | 2 | 1 | 0 | 1 | 1 | (50.0) |
| 7.00 | 93 × 77*B* | 3401824 | 5 | 4 | 4 | 2 | 1 | 1 | 2 | (50.0) |
| 8.00 | 73 × 93*A* | 3401817 | 37 | 19 | 19 | 16 | 2 | 1 | 3 | 15.8 |
| 10.00 | 37 × 77*B* | 3401825 | 5 | 4 | 4 | 3 | 0 | 1 | 1 | (25.0) |
| 10.25 | 71 × 71*B* | 3401818 | 169 | 114 | 103 | 89 | 9 | 5 | 14 | 13.6 |
| 10.75 | 93 × 73*A* | 3401826 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | (100.0) |
| 11.00 | 53 × 77*A* | 3401827 | 5 | 2 | 2 | 0 | 2 | 0 | 2 | (100.0) |
| 13.25 | 25 × 25*C* | 3402081 | 200 | 4 | 2 | 1 | 0 | 1 | 1 | (50.0) |
| ... | Totals | ... | ... | 209 | 193 | 164 | 18 | 11 | 29 | 15.0 |
| Fresh | 2 × 2 | 3401 | ... | ... | 191 | 191 | 0 | 0 | 0 | 0.0 |

* Letters *A*, *B*, *C* designate separate flowers used as males.

The mutations from aged pollen involved the whole plant; that is, they were of the sort to be expected if the mutations were brought in by one of the gametes, and were not the sectorial type of mutation found when seeds are aged or otherwise treated.[2] Two sectorial mutations, one among the test plants and one among the controls, were also found. Since it is most likely that these originated in the seeds after fertilization the plants concerned are not recorded. Spontaneous sectorial mutations may be expected, in this material, to occur in about 0.3% of the plants. The data in table 2 are based upon one-flower samples, but two or more flowers have been recorded for all except two of the plants which showed mutations. It is, of course, in the case of a given mutation, not possible to say whether the

mutation occurred in the male or in the female gamete; or whether the mutation was induced by the treatment, or would have occurred without treatment. However, in Line 1 Datura material, spontaneous non-sectorial pollen abortion mutations occur about one per 500 plants, so that the chances that more than one or two of the 29 mutations found have this origin are very remote. The present investigation furnishes added evidence to that in an earlier publication[4] which indicated that gametic lethals do not occur in plants. The mutative changes responsible for the pollen abortion here found may be supposed to have entered the plants through the sperm cells of the aged pollen grains.

The method of increasing mutation rates by aging of the pollen for a few days seems to be one that might be employed in any material of which the pollen can be stored. A large proportion of dicotyledonous plants will, probably, yield viable pollen after much longer aging than that here reported, judging from the report of Holman and Brubaker.[5] Correns[6] aged pollen of Mercurialis for 120 days, and showed that aged pollen gave progenies with altered sex-ratios. Hiorth[7] kept Antirrhinum pollen alive for 28 days at room temperature, and from it obtained several hundred $F_1$ plants, but grew only four $F_2$ progenies which produced no visible gene mutations. He found that heating pollen to near the lethal point gave no increase in the rate of visible gene mutation.

Mutations which occur in the mature pollen grains may be of particular interest because the simplicity, accessibility and durability of this material seem to make it especially useful for studies on the nature and incidence of mutation. It seems possible also that mutations in nature may be dependent, to an unsuspected extent, upon the conditions to which the pollen has been subjected before it functions in fertilization. The considerable number of mutations found in the experiments here described supports the suggestion of Navashin,[8] in regard to the chromosomal mutations induced by aging seeds—that the metabolic conditions within the cell rather than external agents may be the cause of such mutations.

[1] Aided by a research grant from the Penrose Fund of the American Philosophical Society.

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# THE PROBABILITY-RESULTANT

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The probability-resultant is the combined effect, on the same measured quality, of several mutually independent constituent factors, each of which factor is given in terms of a probability-distribution, and which probability-resultant also is computed in terms of a probability-distribution of the same measured quality among the subject population.

The purpose of this paper is to demonstrate the principles which underlie the computation of such a combined effect.

*The Problem.—Given:* A number ($n$) of distinct prediction-bases ($M_1$, $M_2$, ... $M_n$), each bearing by probability ($K$) upon the same thing-predicted ($R$).[1] That is, given $K = f_1(M_1, R)$, $K = f_2(M_2, R)$, ... $K = f_n(M_n, R)$.

*Find:* $K = f(M_1, M_2, \ldots M_n, R)$ which is the probability-resultant as herein defined.

It is assumed for the time being that these several $M$'s, or prediction-bases, while bearing consistently upon the same $R$, or thing-predicted, are mutually independent of each other. Such independence is fundamentally important.

*Solution.*—The present studies, while general in pattern and application, are based upon the genetics of racing capacity in the Thoroughbred horse. The main reason for such basis is that the Thoroughbred records are exact quantitatively—like the c. g. s. system of physics—in the description of the several race-performances of each individual horse; they are accurate in pedigree or kinship-data; they are extensive; and they are available for use. In fact the records of both performance and breeding of the Thoroughbred horse are kept like the observation notes in some meticulous study in quantitative physiology, as though the Thoroughbred horse were bred and raced actually for scientific study, instead of primarily for "the sovereign sport of horse racing."

*The Resultant Probability* $K = f(M_{1,2,3,\ldots n}, R)$.—The thing reported now is the discovery of the correct way to compute ($K$) the probability-resultant of a group of several ($M$'s) pieces of independent probability prediction-evidence. Each of these several constituent factors ($M$'s) when taken independently must be related definitely as a causal factor or a correlated value of the same ($R$) or thing-predicted.

In the present example this principle concerns the prediction of racing capacity which will be developed in a particular random-selected or pre-

indicated Thoroughbred foal, based upon $n$ independent prediction-bases of or correlations with the said thing-predicted. Herein an $M$, that is, a prediction-basis, is generally the racing capacity of one definitely named individual among the subject foal's nearest blood-kin.

Given a definite kinship, such as that of sire-foal, with the definitely computed specific Manerkonic formula for this particular kinship; ignore all other speed-influencing-or-correlated-factors so as to provide for their random inclusion or complete cross-sectioning in the analysis; we can then readily plot the definite probability-curve for the distribution of racing capacity in the offspring of sires of any given definite racing capacity. Such distribution is called a piece of independent probability-evidence.

The single independent prediction may not be very good, that is, the prediction-curve may be low and flat, but it is definite, and all other factors being completely and randomly cross-sampled, it adds something very definite in the direction of truth.

*Example as Figured on the Accompanying Chart.*—The general formula $K = f(M, R)$—"the Manerkon"—is first worked out specifically for each of the $n$ (in this case four) different factors which bear upon, or are elements of, the same thing-predicted ($R$), which in the present case is Racing Capacity ($RC$) in the pre-selected Thoroughbred foal. However, the prediction-bases ($M$) must in each of the four cases be distinct; the evidence must not be on the same basis, that is, it must not be drawn by the same rules in the shape of four successive samples from the same population; these four pieces of evidence must, of course, refer to the same $R$ or thing-predicted, but must be based upon four distinct $M$'s or prediction-bases, all other factors being randomly represented. This element of independence among the several $M$'s—or bases-of-evidence—is just as essential in probability-mathematics as in law, if truth is the thing sought.

*Rules of Procedure.*—1. All probability-distributions, both constituent and resultant, are analyzed and plotted in the same frame of coördinates $K = f(R)$, in which both $K$ and $R$ are constant—each in its own stuff and scale.

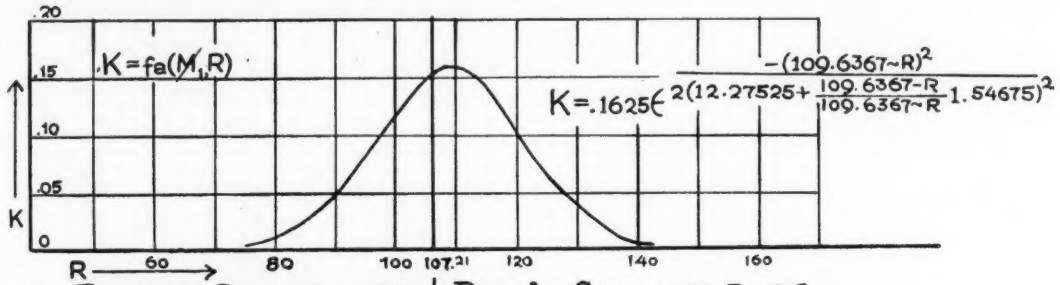
2. The letter $q$ measures the width in $R$-units of each of the several vertical probability-strips. The summation of these strips constitutes the area under the particular probability-distribution curve. This area always equals 1.000.

3. These $n$ bases of evidence ($M$'s), as probability-distributions which bear upon the same thing-predicted ($R$), are superimposed, both mathematically and graphically, one above the other in the same frame of coördinates $K = f(R)$. And the boundary curve of their summation area is of the type shown in the accompanying diagram.

4. *The Shrinkage Axes.*—The coördinates $K$ and $R$.

## THE PROBABILITY-RESULTANT OF SEVERAL INDEPENDENTLY OBSERVED PROBABILITY-EVIDENCES

An example of the General Pattern Formula applied to a case which consists of four pieces of mutually independent probability-evidence—that is, as a case with four different $M$'s or prediction-bases—in reference to the same $R$ or thing-predicted, all other speed-influencing factors being randomly represented.




1. Racing Capacity of the Dam's Sire = 117.5 = $M_1$

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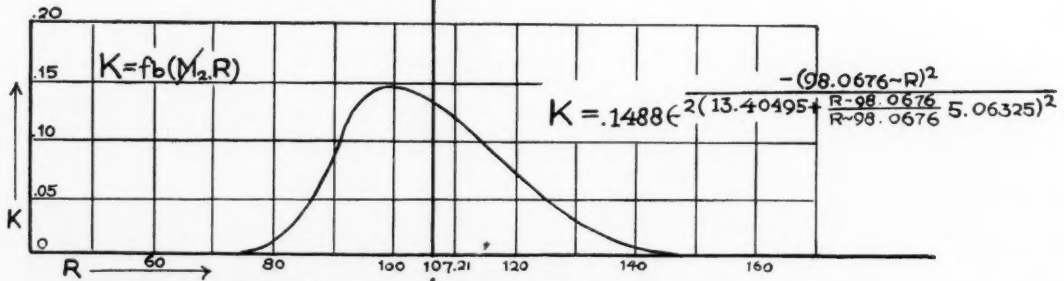
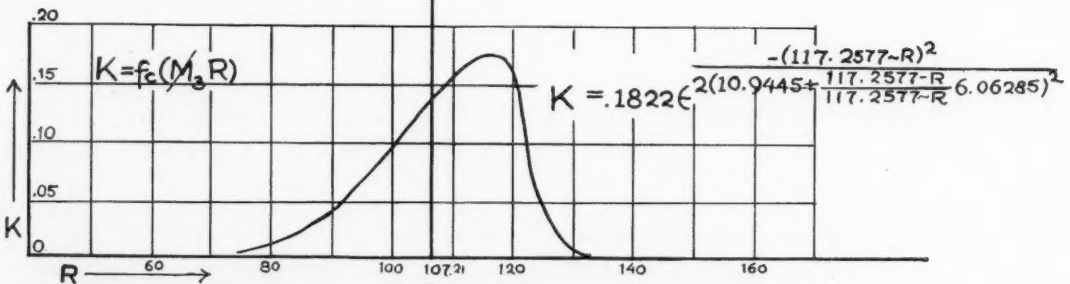
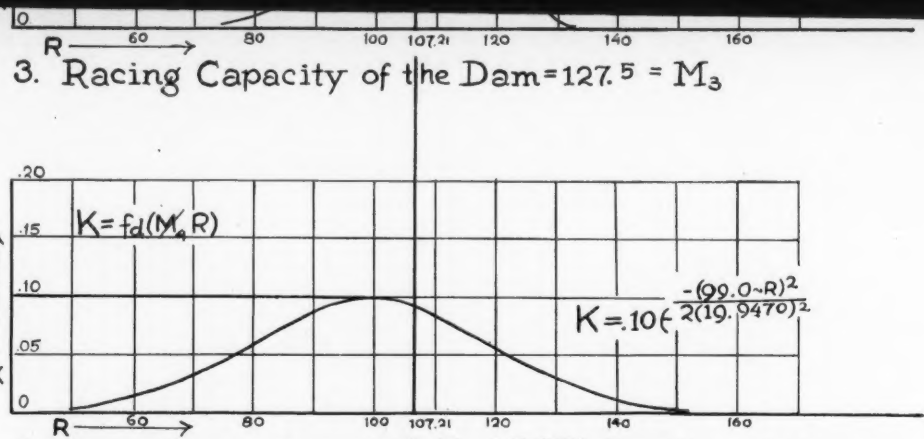



2. Racing Capacity of the Sire = $97.5 = M_2$

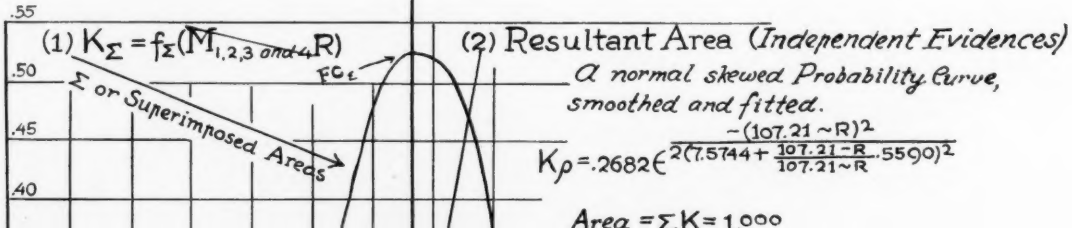


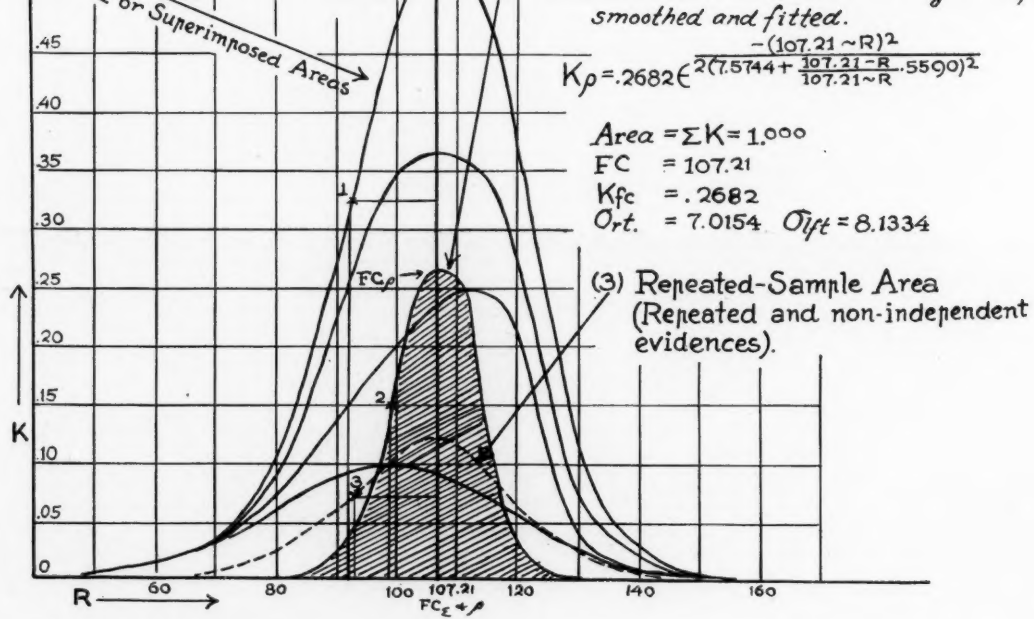

3. Racing Capacity of the Dam = $127.5 = M_3$




3. Racing Capacity of the Dam = 127.5 = $M_3$

4. Any other independent $K = f(M,R)$ Quality whatsoever = $M_4$






PROBABILITY-RESULTANT (Shaded Area).

Shrinkage Axes: $K$—unchanged throughout.

$R$—zero is changed to $R$-locus of highest common probability ($HCP$) = 107.21.

1. Summation Area = $n \cdot 1.000 = n = 4.000 = K$-summation of all vertical strips ($q$ = $R$-units width. Herein $q = 5$) under the $\Sigma$-area curve.

2. Resultant Area (if the four pieces of evidence are mutually independent) = 1.000 = $K$-summation of all such vertical strips under the "Shaded Area" boundary curve.

3. Repeated-Sample Area (if the four pieces of evidence are not mutually independent, but are simply repeated samplings from the same $M$ throughout) = 1.000 = $K$-summation of all such vertical strips under the "dotted curve."

The new zero point on the $R$-coördinate is at the $R$-locus of the vertical line of the highest common probability (*HCP*) of the probability-resultant-area. Except for this relocation of the zero point in the $R$-axis, the $K$ and the $R$ axes of the resultant area are the same as in the several constituent areas.

*The Highest Common Probability (HCP).—(a) Outline for finding the R-locus of HCP by the calculus.—The highest common probability* is a value on the $K$-scale; it should not be confused with $FC_{\Sigma \text{ and } P}$ which is a point on the $R$-scale locating the center of the $q$-class within which the *HCP* falls.

$FC_{\Sigma \text{ and } P}$ is the fluctuation-center on the common $R$-scale of the summation of probability-values, and it is also the $R$-locus of $K_{fc_P}$ or the *highest common probability* of any $R \pm \frac{q}{2}$ class-range of the thing-predicted, within the resultant-probability-distribution.

In the accompanying example (see diagram) the several independent probability-distributions are plotted on the same $R$-scale, and each with the same but independently based $K$-scale. Both approximately by the graphical method, and accurately by the calculus, there is found the $R$-point directly above which the slope of the summation probability curve equals zero.

$K = f_P(M_{1,2,3 \text{ and } 4}, R)$. Since each $M$-value and its corresponding cross-section (i.e., its probability-distribution of $R$ for the particular $M$-value) is given, each such cross-section, that is, each individual $K = f(R)$ can be and is herein fitted into the common coördinates $K$ and $R$ (of necessity, the "same $R$-stuff and $q$-class range," and for convenience the same $K$ and $R$-scales) (see curves for $M_1$, $M_2$, $M_3$ and $M_4$ in the diagram). $K = f_P(R)$ = the probability-resultant of the four specific constituent Manerkonic cross-sections shown in the diagram as four pieces of mutually independent probability-evidence.

Note that for the summation curve, the point, exactly above the $FC_{\Sigma \text{ and } P}$ on the $R$-scale, is the locus of that point on the curve where the slope equals zero. According to the rules of calculus the point on a curve at which the slope equals zero is either the maximal or minimal value of such curve (depending on the test). In the present case it is obviously at the maximal value where the slope equals zero.

Before application of the rules of the calculus, it will be convenient in the present case to take the logarithms of each side of the four constituent equations. This step will in no way affect the value of $R$ after summation of the log derivatives, which gives the resultant slope equal to zero.

Find the first derivatives of each of the four simplified constituent equations which make up the composite curve which supplies the resultant

slope, and summate them. This summation is equated to zero, and the equation solved for $R$.

*Value.*—Having applied these rules of calculus to the present case and found $R = 107.21$, we conclude that, in the resultant-probability curve, with all constituent evidence duly weighted, the highest common probability, which is also the resulting fluctuation-center of offspring values, lies at the center of the class-range of racing capacity, $R = 107.21 \pm 2.5$.

This resulting fluctuation-center is also designated as $FC_{\Sigma \text{ and } P}$.

(*b*) *The Absolute Numerical K-value of the HCP.*—$K_{fc\rho}$ = the actual $K$ or probability-value of this resultant-highest common probability.

$$K_{fc\rho} = \frac{\Sigma \text{ constituent } K\text{'s at } FC}{\sqrt{n}}.$$

$n$ = number of independent constituent probability-evidences in the resultant. In this case $K_{fc\rho} = \frac{0.5364}{\sqrt{4}} = 0.2682$.

$P$, $p$ or $\rho$ in the formulae or on the diagram refers to the probability-resultant in particular contrast to $\Sigma$ on the diagram or in the formula for the summation or cumulative area.

5. *Relative "Right and Left" Areas, Skewness and Standard Deviation.*—$\sum AP_{l \text{ or } r}$ = the summation, in the final resultant-probability-distribution, of all those probabilities (or area-portions) supplied by all constituent pieces of probability-prediction-evidence (Manerkonic cross-sections actually used), which, on the same $R$-scale, in one lot fall cumulatively to the left, and in another to the right of the *HCP*, constitute, in the smoothed probability-resultant-curve the bases for the respective left and right standard deviations.

In the present example summation area to the left of *HCP* = 0.5691 of the total; summation area to the right = 0.4309 of the total.

When total area = 1.000 and $K_{fc} = 0.2682$, $\sigma_{\text{symmetrical}} = 7.5744$.

But, based on relative areas, in the present case

$\sigma_{\text{lf.}} : \sigma_{\text{rt.}} = 0.5691 : 0.4309$.

$\sigma_{\text{left}} + \sigma_{\text{right}} = 2\sigma_{\text{symmetrical}} = 15.1488$.

Dividing 15.1488 proportionately gives $\sigma_{\text{lf.}} = 8.1334$ $R$-units, and $\sigma_{\text{rt.}} = 7.0154$ $R$-units.

6. *Shrinkage.*—In the present example $n = 4$. Assuming complete independence among the $n$ (in this case 4) $M$'s as prediction-bases for the same $R$, the several constituent curves are superimposed both graphically and mathematically as shown in the diagram. Now as a probability-resultant the main difficulty with this composite area is that it is just $n$ (in this case 4) times too great; its slope or type, its position and its skewness are correct as the probability-resultant of the four given pieces of independent-probability-prediction evidence.

According to the rules of plane geometry, two similar areas are to each other as the squares of their homologous lines. It is obvious then that with the correct shrinkage-axes in hand, and with the necessity to shrink the summation area, which equals $n$, to a similar area which equals 1.000, such shrinkage may be mathematically accomplished as follows:

Find the $K$ and the $R$ coördinate values of any point on the summation curve (boundary of the composite area). Divide each of these values by the square root of $n$. As coördinates these new values locate the corresponding point on the probability-resultant curve. Trace the new probability-resultant curve by representative points located in the foregoing manner.

7. *Pattern Formula.*—$K_p$ is the probability that the pre-indicated individual will fall within the pre-selected class-range of $R \pm \frac{q}{2}$ units on the common $R$-scale.

The general or pattern formula for such probability-prediction thus becomes:

$$K_p = K_{fcp} \epsilon^{\frac{-(FC \sim R)^2}{2\left(\frac{0.3989 \cdot q}{K_{fcp}} \cdot \Sigma AP_{r.\text{ or }l.} \cdot 2\right)^2}}$$

This Pattern Formula represents a form of the curve which bounds the basic-probability-distribution area, $K = y_0 \epsilon \frac{-x^2}{2\sigma^2}$. The conversion of all basic data into the above elementary probability structure is the major objective of all observations and analyses.

For this newly delimited and smoothed "skewed-normal-probability-resultant-distribution" area the following basic values have been found:

1. Area = 1.000.
2. $q = 5$ $R$-units.
3. $FC_p = 107.21$.
4. $K_{fcp} = 0.2682$.
5. $\Sigma AP_l = 0.5691$ of total.
6. $\Sigma AP_r = 0.4309$ of total.
7. $\sigma_{\text{left}} = 8.1334$.
8. $\sigma_{\text{right}} = 7.0154$.

*Note on Non-Independence of Prediction-Bases.*—The correct resulting probability-distribution area will be very different from the "probability-resultant area" in case the $n$ (herein 4) pieces of evidence are simply repetitions—not independent but based upon the same $M$; that is, simply different samples drawn by the same rules from the same population. The definition of independence thus becomes of very substantial importance,

and in genetics the several distinct kinships prove to be amply distinct to constitute the subjects of pieces of such independent evidence. Thus the racing capacities involved in the sire-foal relationship constitute one piece of independent probability-evidence; the dam-offspring relationship another; the sire's sire another; and so on. Each piece of such probability-prediction-evidence constitutes a definite component in the resultant prediction-formula.

While the term "probability-resultant" is reserved to describe the set-up when the constituent probabilities are completely independent in their bases, the term "probability-repetant" will be used to describe the resulting area when evidence is not independent but is only repeated samplings of the same thing, from the same population, by the same selection-rules.

Whether the independence is complete, or there is only a little overlapping, or there is complete overlapping or duplication, the first five steps of procedure as herein outlined are the same; the piling up of the several constituent distribution-areas in the same coördinate frame is the same; the shrinkage axes are the same; the relative skewness from the normal probability curve is the same.

But there is a fundamental and vast difference in the sixth point, the shrinkage rules, and consequently in the height of the resulting curves and consequently in their spread. In the case of complete overlapping or duplication in the nature of the several $M$'s, the spread, that is the $R$-scale, is unchanged from the base scale of the summation area. But the line of highest common probability in the resulting repetant-area is to the height of the $K_{fc}$ of the summation area as 1 is to $n$.

There is thus in duplicate evidence, only a vertical shrinkage to $\frac{1}{n^{\text{th}}}$, but no lateral shrinkage; while with independent evidences the summation-area is shrunk toward each of the axes ($K = 0$, and $R = 0$ at the locus of $HCP$) so that the resultant-area equals $\frac{1}{n^{\text{th}}}$ of the summation-area, but the shape is unchanged.

*Partial Independence, Partial Overlapping.*—In any case as a consequence of the several constituent probability-distributions—the several $M$'s—not being independent—that is, overlapping or being duplicates more or less, the resulting synthesized curve, while it must always have an area equal to 1.000, will be somewhere in shape between the resultant-probability-curve and the repetant-probability-curve (see diagram).

*Current Work.*—In the case of "some-but-not-how-much" known overlapping, current researches have in view the discovery of the principles which may measure the degree of independence of prediction-bases. The method under test is to compare the actual-population-distribution-deter-

mined-by-census with the population-distribution as predicted by the resultant-probability formula, for measuring the degree of independence and the degree of overlapping.

The current analyses—in reference to Thoroughbred horses in their individual qualities and pedigree kinships—while made on living forms have been duplicated according to the derived formulas very exactly by dice-casting and ball-drawing experiments.

*Summary.*—When the several probability-evidences are independent, besides providing the probability-resultant, which is the main thing sought, the new formula $K = f$ (the several constituent probability-distributions) as herein given, has the following properties:

(*a*) Regardless of its value, every piece of constituent probability-evidence, which is in hand in reference to any definitely related prediction-basis, is used and correctly stressed in the resultant.

(*b*) The probability-resultant piles up evidence of probable offspring or *R*-values, but it is not simply an equable piling-up of all probabilities. Mathematically—as in common sense and in legal testimony—predicted-values with a high *K* or probability of occurrence (as rated independently by each of several independent *M*'s, that is, by the several constituent pieces of independent probability-evidence), tend in the probability-resultant to become still more probable, while *R*-values with low probabilities among the constituents tend to become still less probable in the resultant.

(*c*) If the *M*'s or prediction-bases are "constant, non-independent, duplicate or overlapping" the resulting probability-repetant area is simply an average of the overlapping constituent probability-areas.

(*d*) This new general or pattern formula for the probability-resultant is especially applicable in genetics for finding the Specific Formula of Heredity for any trait or quality which is measurable in the individual and which to any degree is shown to run-in-the-family.

(*e*) This general principle of the probability-resultant is also equally applicable to problems in physics and other sciences—whenever a number of independent measured *M*'s or prediction-bases are, in any measured manner, related to a common measured *R* or thing-predicted.

Thus the specific formula for the probability-resultant, which was discovered in connection with researches on the genetics of the Thoroughbred horse, proves to be a General or Pattern Probability-Prediction Formula.

*Description of the Two Accompanying Formulae-Tables.*—These formulae concern the three areas indicated on the accompanying diagram as 1. Cumulative Area; 2. Probability-Resultant Area; 3. Probability-Repetant Area.

*Table 1.*—This table is presented in two sections. Section 1 gives the specific formulae which fit the present example; and Section 2 gives the generalized or pattern formulae for each of the three subject curves.

TABLE 1, SECTION 1

SPECIFIC FORMULAE

1. (*a*) Cumulative Area

$$K_c = 0.1625\ \epsilon^{\frac{-(109.64-R)^2}{2(12.275\pm 1.547)^2}} + 0.1488\ \epsilon^{\frac{-(R-98.07)^2}{2(13.405\pm 1.547)^2}} + 0.1822\ \epsilon^{\frac{-(117.26-R)^2}{2(10.944\pm 6.063)^2}} + 0.10\ \epsilon^{\frac{-(R-99.0)^2}{2(19.95)^2}}$$

(*b*) Smoothed Cumulative Area

$$K_{c_s} = 0.5364\ \epsilon^{\frac{-(107.21-R)^2}{2(15.1488\pm 1.1181)^2}}$$

2. (*a*) Resultant Area

$$K_P = 0.0813\ \epsilon^{\frac{-(216.85-2R)^2}{2(12.27\pm 1.547)^2}} + 0.0744\ \epsilon^{\frac{-(2R-205.28)^2}{2(13.405\pm 5.063)^2}} + 0.0911\ \epsilon^{\frac{-(224.47-2R)^2}{2(10.944\pm 6.063)^2}} + 0.05\ \epsilon^{\frac{-(2R-206.21)^2}{2(19.95)^2}}$$

(*b*) Smoothed Resultant Area

$$K_{P_s} = 0.2682\ \epsilon^{\frac{-(107.21-R)^2}{2(7.5744\pm 0.5590)^2}}$$

3. (*a*) Repetant Area

$$K_R = 0.0406\ \epsilon^{\frac{-(109.64-R)^2}{2(12.275\pm 1.547)^2}} + 0.0372\ \epsilon^{\frac{-(R-98.07)^2}{2(13.405\pm 5.063)^2}} + 0.0456\ \epsilon^{\frac{-(117.26-R)^2}{2(10.944\pm 6.063)^2}} + 0.025\ \epsilon^{\frac{-(R-99.0)^2}{2(19.95)^2}}$$

(*b*) Smoothed Repetant Area

$$K_{R_s} = 0.1341\ \epsilon^{\frac{-(107.21-R)^2}{2(15.1488\pm 1.1181)^2}}$$

TABLE 1, SECTION 2

GENERAL FORMULAE

1. (*a*) Cumulative Area

$$K_c = K_{fc1}\,\epsilon^{\frac{-(FC_1-R)^2}{2[\sigma_{s_1}\pm(\sigma_{s_1}-\sigma_{R1})]^2}} + K_{fc2}\,\epsilon^{\frac{-(FC_2-R)^2}{2[\sigma_{s_2}\pm(\sigma_{s_2}-\sigma_{R2})]^2}} + K_{fc3}\,\epsilon^{\frac{-(FC_3-R)^2}{2[\sigma_{s_3}\pm(\sigma_{s_3}-\sigma_{R3})]^2}} + \ldots\ K_{fcm}\,\epsilon^{\frac{-FC_m-R)^2}{2[\sigma_{s_m}\pm(\sigma_{s_m}-\sigma R_m)]^2}}$$

where $\sigma_s = \dfrac{q}{K_{fc}\sqrt{2\pi}}$ and $\sigma_R = \dfrac{AP_r - q}{K_{fc}\sqrt{2\pi}}$

(*b*) Smoothed Cumulative Area

$$K_{c_s} = K_{fc\Sigma}\,\epsilon^{\frac{-(FC_\Sigma-R)^2}{2[\sigma_{s_c}\pm(\sigma_{s_c}-\sigma R_c)]^2}}$$

2. (*a*) Resultant Area

$$K_P = \frac{K_{fc1}}{\sqrt{n}} \epsilon^{\frac{-\{FC_1 - [R + (\sqrt{n} - 1)(R - FC\Sigma)]\}^2}{2[\sigma_{s_1} \pm (\sigma_{s_1} - \sigma_{R1})]^2}}$$

$$+ \frac{K_{fc2}}{\sqrt{n}} \epsilon^{\frac{-\{FC_2 - [R + (\sqrt{n} - 1)(R - FC\Sigma)]\}^2}{2[\sigma_{s_2} \pm (\sigma_{s_2} - \sigma_{R2})]^2}}$$

$$+ \frac{K_{fc3}}{\sqrt{n}} \epsilon^{\frac{-\{FC_3 - [R + (\sqrt{n} - 1)(R - FC\Sigma)]\}^2}{2[\sigma_{s_3} \pm (\sigma_{s_3} - \sigma_{R3})]^2}}$$

$$+ \ldots$$

$$+ \frac{K_{fcm}}{\sqrt{n}} \epsilon^{\frac{-\{FC_m - [R + (\sqrt{n} - 1)(R - FC\Sigma)]\}^2}{2[\sigma_{s_m} \pm (\sigma_{s_m} - \sigma_{R_m})]^2}}$$

(*b*) Smoothed Resultant Area

$$K_{P_s} = \frac{K_{fc\Sigma}}{\sqrt{n}} \epsilon^{\frac{-(FC\Sigma - R)^2}{2\left[\frac{\sigma_{s_c}}{\sqrt{n}} \pm \left(\frac{\sigma_{s_c}}{\sqrt{n}} - \frac{\sigma R_c}{\sqrt{n}}\right)\right]^2}}$$

3. (*a*) Repetant Area

$$K_R = \frac{K_{fc1}}{n} \epsilon^{\frac{-(FC_1 - R)^2}{2[\sigma_s \pm (\sigma_{s_1} - \sigma_{R1})]^2}} + \frac{K_{fc2}}{n} \epsilon^{\frac{-(FC_2 - R)^2}{2[\sigma_{s_2} \pm (\sigma_{s_2} - \sigma_{R2})]^2}}$$

$$+ \frac{K_{fc3}}{n} \epsilon^{\frac{-(FC_3 - R)^2}{2[\sigma_{s_3} \pm (\sigma_{s_3} - \sigma_{R3})]^2}} + \ldots \frac{K_{fcm}}{n} \epsilon^{\frac{-(FC_m - R)^2}{2[\sigma_{s_m} \pm (\sigma_{s_m} - \sigma_{Rm})]^2}}$$

(*b*) Smoothed Repetant Area

$$K_{R_s} = \frac{K_{fc\Sigma}}{n} \epsilon^{\frac{-(FC\Sigma - R)^2}{2[\sigma_{s_c} \pm (\sigma_{s_c} - \sigma_{Rc})]^2}}$$

The delimiting curve of each of these three areas has two aspects:

(1) The area and curve which result from superimposing one constituent area above another in the same 2-dimensional coördinate frame; or an area and curve which result from shrinking this cumulative area according to certain definite rules.

(2) The second member of each pair of formulae is called the Formula for the Fitted or Smoothed Area. In case the cumulative area resembles closely a normal probability curve with a certain degree of skewness—

which close resemblance is practically very certain—the cumulative curve is fitted and smoothed to a skewed probability pattern.

Thus any tendency to bimodalism or multimodalism which might have appeared in the cumulative curve is ironed out. But in case any such irregularity is so substantial or persistent that it might reflect a real causal factor the analysis should continue from the cumulative area and formula rather than from their smoothed and fitted aspects.

*Table 2.*—This table gives, for convenient reference, the comparative structural and numerical properties of the three specific smoothed and fitted probability-areas.

TABLE 2

COMPARATIVE QUANTITIES WHEN THE THREE CURVES (1, CUMULATIVE AREA; 2, RESULTANT AREA; 3, REPETANT AREA), ARE SMOOTHED OR FITTED TO A SKEWED NORMAL DISTRIBUTION AREA

| | 1. CUMULATIVE AREA | 2. RESULTANT AREA | 3. REPETANT AREA |
|---|---|---|---|
| Area or $n$ | 4 | 1 | 1 |
| $q$ in terms of $R$-units | 5 | 5 | 5 |
| $FC$ location on $R$ scale | 107.21 | 107.21 | 107.21 |
| $K_{fc}$ in terms of $K$ | 0.5364 | 0.2682 | 0.1341 |
| Area left of $FC$ in terms of % | 53.69 | 53.69 | 53.69 |
| Area right of $FC$ in terms of % | 46.31 | 46.31 | 46.31 |
| $\sigma$ left in terms of $R$ | 16.2669 | 8.1334 | 16.2669 |
| $\sigma$ right in terms of $R$ | 14.0308 | 7.0154 | 14.0308 |

NOTES:

The frame of the coördinates, $R$ and $K$, remains unchanged throughout.

In shape the cumulative area and the resultant area are the same. The repetant area is at every $R$-point $\frac{1}{n}$-th as tall as the cumulative area.

[1] Laughlin, H. H., "The General Formula of Heredity," *Proc. Nat. Acad. Sci.*, **19**, 787–801 (1933); Laughlin, H. H., "The Specific Formula of Heredity," *Ibid.*, **19**, 1020–1022 (1933).

# HOW TO USE THE SPECIFIC FORMULA OF HEREDITY

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The use of the Specific Formula of Heredity will be demonstrated by a specific example which applies the recently discovered formula to the probability-prediction of adult stature of an individual in that section of the British people sampled by Sir Francis Galton in his classical stature-study, 1884–1889.

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$K = f(M, R)$ *Given* $M$; select $R$ arbitrarily; find $K$.

*Example.*

Given: Father's stature *70.5*, Mother's stature *65.8* } The foundation of $M$ or the prediction-basis.

$$\frac{\text{(Father's adult height in inches} + \text{Mother's adult height in inches} \times 1.08)}{2} = \text{Mid-parental stature} = 70.78''$$

Find: Probability ($K$) that an adult son will develop a stature of, say, $73 \pm 0.5''$.

$R$ is any arbitrarily selected adult stature—the thing-predicted in inches $\pm 0.5''$.

$M$ = Mid-parental stature minus 68.54. $M = 2.24$ $M^2 = 4.916$

Note that $M$ is the prediction-basis throughout and that every factor in the resultant formula is a function of $M$.

(1) Find $FC$ by substituting $M$ and $M^2$ in:

$$FC = f(M) = [0.5377M + 0.1252M^2]\left(\frac{M + (M-0)}{2M}\right)$$

$$[0.1590M - 0.0913M^2]\left(\frac{M-(M-0)}{2M}\right) - 0.6548 \ldots FC = 1.07315$$

(2) Find $K_{fc}$ by substituting $M$ and $M^2$ in:

$$K_{fc} = f(M) = 0.0035M + 0.0014M^2 + 0.1785 \ldots K_{fc} = 0.1932$$

(3) Find $\sigma_1$ by substituting $M$ and $M^2$ in:

$$\sigma_1 = f(M) = 0.0314M + 0.0052M^2 + 2.0712 \ldots \sigma_1 = 2.16711$$

(4) Find $\sigma_s$ by substituting $M$ and $M^2$ in:

$$\sigma_s = \frac{1}{2.5066K_{fc}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \sigma_s = 2.06494$$

Now substituting the above found numerical values of these several functions of $M$ in the formula:

$$K = K_{fc} \in^{\frac{-(FC \sim R)^2}{2\left[\sigma_s + \frac{(\sigma_s - \sigma_1)(FC - R)}{(FC \sim R)}\right]^2}}$$

it is found that $\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots K = 0.1072$

Based upon the generalized evidence of the 1028 actual cases, this particular probability-value is the "soundest mathematical judgment" which at present we know how to render for the given problem.

*Note on Graphical Computation.*—The foregoing method of substitution is, of course, the proper procedure for finding the correct values required by the particular Manerkonic formula, but, in case the particular Manerkonic model is in hand, the graphical computation of $K = f(M, R)$ is sometimes useful also as a check or an approximation. This graphical value is found as follows: Given any selected $M$ and $R$, locate the Manerkonic-surface-point common to the given $M$ and $R$; then read the coördinate value of $K$ on the "post" which carries the $K$-scale. (See illustration: Manerkonic model.)

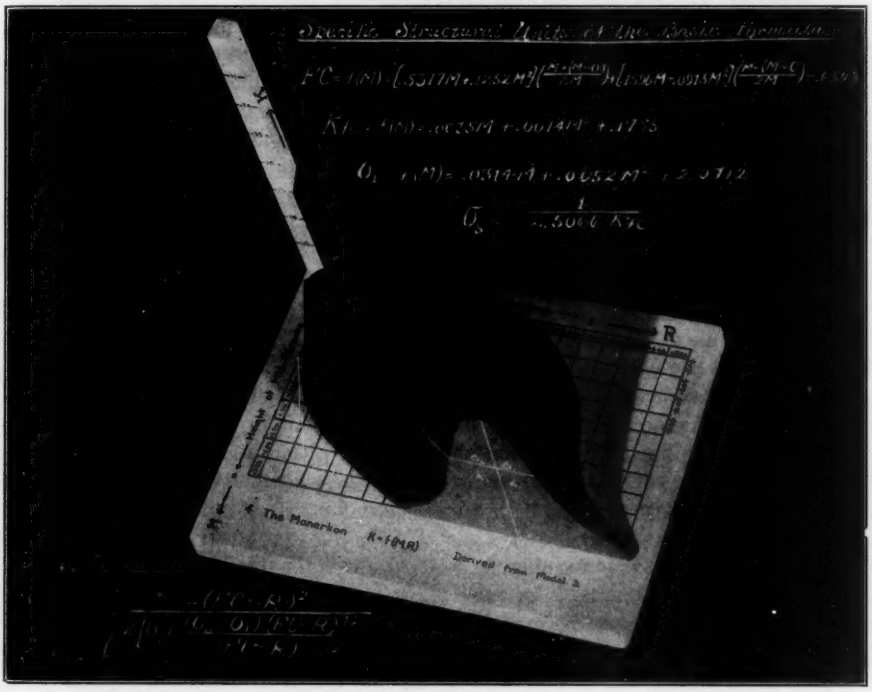
*The Sex Factor in Stature.*—Galton made his stature-study on the male basis. In his analysis he followed the rule: Female adult stature times 1.08 gives the adult male stature-equivalent, so far as the hereditary growth-factor is concerned. Consequently if it were required by the present specific Manerkonic probability-prediction-formula to find the probability ($K$) that a random-selected daughter (not a son) derived from the given particular mid-parental stature-value would develop an adult stature of $73 \pm 0.5$ inches, it would be equivalent to requiring the computation of the probability that a son would develop the adult stature ($73 \cdot 1.08$) $\pm$ 0.5 inches; or if it were required to find the probability that a daughter would develop an adult stature equivalent so far as heredity is concerned to that of a son with an adult stature of $73 \pm 0.5$ inches, this would be the same biologically as requiring the computation of the probability that the daughter would develop an adult stature of $(73 \div 1.08) \pm 0.5$ inches.

*The Nature of Data Needed.*—For the Construction of a Specific Probability-prediction-formula—a Manerkon, $K = f(M, R)$.

The General Formula of Heredity[1] supplies the general pattern. By following this pattern with adequate specific first-hand data the Specific Formula, or Manerkon, is readily computed. This will be specific and directly usable as a probability-prediction-formula in reference to the

particular quantitatively measured subject-trait or quality within the particular population sampled, so far as such subject-trait $R$ depends upon the particular selected $M$ or prediction-basis.

*Number of Data Needed.*—In the construction of a specific Manerkon,




Manerkonic Model: Reprinted from *Proc. Nat. Acad. Sci.*, 19, 1021, Dec., 1933.

$K = f(M, R)$, the mathematical formula and model of the Specific Formula of Heredity which, based upon $(M)$ the stature of the father and the stature of the mother, predicts by $(K)$ a definite probability that the adult stature of the offspring, corrected for sex, will fall within any selected stature $(R) \pm 0.5$ inch. It is a specific application of the General or Pattern Formula of Heredity to a given case.

This particular Specific Formula presents the soundest generalized judgment at present available, based upon the evidence of Galton's 1028 first-hand stature measurements of adult children and of the father and mother of each adult child, within a definite section of the British people, 1884–1889.

that is, a probability-prediction formula $K = f(M, R)$, fewer than one thousand cases of measured values of $M$ the prediction-basis and $R$ the thing-predicted will not suffice.

*Present Progress.*—The construction of a satisfactory Manerkon was possible in the case of Galton's classical stature-study because Galton had

collected 1028 stature-measures for both $M$ the adult mid-parent, and $R$ the adult child, and had corrected the data satisfactorily for sex differences. Galton, however, did not apply the present probability-prediction methods to the analysis of his data; these principles were discovered and made available in 1933; Galton's classical data were collected in 1884–1889.

In researches on the genetics of racing capacity in the Thoroughbred horse, a number of Manerkonic formulae have been constructed—one for each selected relationship between a specific ancestral blood-kinship and the foal. For each Manerkon a few more than one thousand cases of $M$ the measured racing capacity in the given ancestor, and of $R$ the measured racing capacity in the foal, were secured as basic data. These particular Manerkonic studies on the specific quality of racing capacity in the Thoroughbred horse cover the following kinships: 1. Sire–Offspring; 2. Dam–Offspring; 3. Sire's Sire–Offspring; 4. Sire's Dam–Offspring; 5. Dam's Sire–Offspring; 6. Dam's Dam–Offspring; 7. Full Sib–Full Sib; 8. Half Sib–Half Sib; 9. Foal–Parent; 10. Grandchild–Grandparent; 11. Uncle or Aunt–Nephew or Niece; 12. First Cousin–First Cousin.

*Note on the q-Value.*—In probability-prediction work, the specific prediction must be that a certain pre-selected individual thing or function will, in reference to the particular measured trait or quality, fall not exactly on a line with no width, but will fall within a certain measured class-range between two no-width lines. The probability of the thing-predicted falling exactly on the line is zero because the line has no $R$-width.

In the Manerkonic formula the letter $q$ stands for the width of the prediction-class in $R$-units. The value of $q$ is an arbitrary matter; it is determined by the practical necessities of the case. For instance, in the present human stature study $q = 1$ inch or 1 $R$-unit, since the stature-scale is in terms of inches, and the range of normal stature in the particular population consists of "ten or fifteen" such 1-inch classes. If the data were fewer or coarser the prediction-class would have to be wider—that is, $q$ would have to equal more than 1 inch, and the whole study would be more crude. If, however, the data were more numerous and more accurate, then the $q$-class could be narrowed down to say a $^1/_2$-inch range. In this case the resultant would be somewhat more refined in reference to its particular trait and population than is the case with the Manerkon as pictured, which was worked out with the one-inch $q$-value.

In the study of racing capacity in the Thoroughbred horse the $q$-class range was taken at "5 pounds." Within the group of racing horses studied in these researches the measure of racing capacity ranges from 65 to 140. In the future it would be desirable to perfect this particular research so that the Manerkonic or prediction-formula could be based on a 1-pound or a 2-pound $q$-class range, and other refinements also included.

*The Number of M and R Classes.*—The number of these classes is determined by the natural range of the subject-trait or quality within the subject population, and the arbitrarily but sensibly and practically selected $q$-value. "Ten or fifteen" such classes are in general a satisfactory number for the computation of a reliable Manerkonic formula out of a thousand data. For each Manerkon the thousand or more cases of specific relationship are duly "cross-sectioned or pigeon-holed." For the ordinary Manerkon it will be found that each of about three-fourths of the cross-sectioned-area-classes will be represented by one or more out of the thousand individuals which comprise the sample. The vacant classes or areas are those in the "uncorrelated class corners" of the $M$ and $R$ relationship.

While in building the Manerkon the $M$-values are of necessity thrown into class-ranges, when the Manerkon is completed and the $M$-classes smoothed into a continuous surface, $M$—as a practical prediction-basis—can henceforth be taken at any exact point. But $R$—the thing-predicted—is never predicted as a point; $R$ must always remain an active class-range—bounded by a definite $R$-point $\pm \frac{q}{2}$.

*One Piece of Prediction-Evidence.*—Each specific Manerkon $K = f(M, R)$ provides, by its cross-section at the selected $M$-point, one piece of constituent probability-prediction evidence for use (in connection with several —that is $n$—similarly appropriate cross-sections, one-each-from-a-total-of-$n$-different-Manerkons) in the computation of the probability-resultant, $K_p = (M_1, M_2, \ldots M_n, R)$, of the $n$ pieces of independent evidence. All evidence in the shape of independent Manerkonic cross-sections, which bear upon the same $R$ or Thing-predicted, can be used in the computation of the probability-resultant. The better the evidence, that is, the more accurate, the more extensive, and the more independence in reference to prediction-basis, the better will be the prediction—that is, the narrower and taller will be the probability-resultant curve. A tall thin probability-area shows good prediction; a low flat cross-section shows poor prediction; but both are equally definite and real in pointing toward the truth. In reference to its prediction-basis each is an accurate mathematical picture of Nature's behavior, and a definite piece of evidence for equitable use in computing the probability-resultant.

*Source of Data.*—In making a specific probability-prediction-formula the principal task ahead is to secure a thousand or more first-hand quantitatively measured data which cover as a fair sample the entire range of both the prediction-basis and the thing-predicted. These data are then adjusted with the minimum amount of mathematical smoothing to give, in the Manerkonic formula and its mathematical model, an accurate mathematical picture of Nature's behavior in the specific case.

When such a Manerkon is completed it becomes of permanent reference

value for the particular measured trait or quality for the particular population sampled. With the specific Manerkonic formula in hand, one can arbitrarily select any $M$-value and any $R$-value, and can then compute $K$, that is, the probability that the ancestor with the selected $M$-value will be associated with the pre-selected $R$-value in the particular pre-selected offspring.

*Future Progress.*—Many such Manerkonic prediction-formulae should be worked out in the fields of plant, animal and human genetics, just as these first Manerkons were worked out for stature in a section of the British people and for racing capacity in the Thoroughbred horse. One of the principal tasks of the Eugenics Record Office of the future is to prepare in its laboratories, and to preserve for ready and permanent reference in its archives, many Manerkonic prediction-formulae for specific measurable human qualities—physical, mental and temperamental.

In this field of research, in reference to a given trait or quality the order of most effective attack is first, yard-stick invention; second, pedigree-analysis of the thing which is first quantitatively measured.

Similarly, other research laboratories of human anthropometry and psychology would serve science if they should work out, and save for reference, accurate Manerkonic formulae for specific measurable structural and functional qualities in definite racial and family-stocks, and other population groups of mankind. Also the laboratories and experiment stations for plant and animal breeding would find it profitable to work out specific Manerkonic formulae of heredity, and to preserve them for their own reference and for exchange with other institutions and research workers. Because the task is too big for any one institution or small group of laboratories, the promotion of agreement on the particular subjects for quantitative yard-stick invention and for Manerkonic analysis by different members would constitute a valuable service for research associations.

In other sciences besides biology, whenever there is a definitely measurable relationship between $M$ the Prediction-basis, and $R$ the Thing-predicted, practical use can be made of the Manerkonic formula, $K = f(M, R)$—that is, $K$ or Probability, is a function of $M$ the Prediction-basis and of $R$ the Thing-predicted. The specific Manerkonic formula finds what this specific function is, and presents it for practical use.

[1] H. H. Laughlin, "The General Formula of Heredity," *Proc. Nat. Acad. Sci.*, **19**, 789–801 (1933); "The Specific Formula of Heredity," *Ibid.*, **19**, 1020–1021 (1933).

# THE PROBLEM OF DIRICHLET FOR AN ELLIPSOID

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Recently C. M. Rigby[2] determined the electrical field produced by a distribution of charge in equilibrium on a conducting sphere lying midway between two parallel conducting planes at zero potential. The present paper treats of a more general problem, in which the sphere is replaced by either an oblate or a prolate ellipsoid of revolution, and thus enables one to analyze the field due to a charged circular disc and thin rod lying between the infinite parallel earthed planes.

The method employed in the solution of this problem consists of constructing a class of harmonic functions which satisfy the boundary conditions on the planes and of suitably combining them so as to satisfy the boundary condition on the surface of the ellipsoid. A suitable generating function of the class of harmonic functions vanishing on the planes $z = \pm h$ is Green's function $V_0(x, y, z; \zeta)$ for the region interior to the planes $z = \pm h$ and the point $(0, 0, \zeta)$, where $|\zeta| < h$. Differentiating $V_0$ $m$-times with respect to $\zeta$, and transforming the variables $x, y, z$ into prolate spheroidal coördinates defined by

$$x = c[(r^2 - 1)(1 - \mu^2)]^{1/2} \cos\varphi, \quad y = c[(r^2 - 1)(1 - \mu^2)]^{1/2} \sin\varphi, \quad z = cr\mu \tag{1}$$

gives, upon setting $\zeta = 0$, a harmonic function

$$V_m(0) = \frac{1}{c} \sum_{n=0}^{\infty} (2n + 1) P_n(\mu) Q_n(r) \left(-\frac{1}{c}\right)^m P_n^m(0) +$$

$$\sum_{p=0}^{\infty} \frac{(m + p)!}{p!} [(-1)^m A_{m+p} - B_{m+p}] c^p \sum_{i=0}^{p} a_{i,p} P_i(r) P_i(\mu), \tag{2}$$

where

$$A_0 - B_0 = \frac{1}{h} \sum_{n=1}^{\infty} \frac{(-1)^n}{n},$$

$$A_q = \frac{1 + (-1)^q}{(4h)^{q+1}} S_{q+1},$$

$$B_q = \frac{1 + (-1)^q}{(2h)^{2q+1}} \left(1 - \frac{1}{2^{q+1}}\right) S_{q+1}, \quad (q = 1, 2, \ldots).$$

$S_q$ is the Riemann zeta function $S_q = \sum_{r=1}^{\infty} r^{-q}$, $P_n(\mu)$ and $Q_n(r)$ are the

Legendre functions of the first and second kinds, respectively, $c$ is a constant, and

$a_{i,n} = \dfrac{(2i+1)2^i n!(n/2+i/2)!}{(n/2-i/2)!(n+i+1)!}$, when $n-i$ is even and non-negative,

$a_{i,n} = 0$, when $n-i$ is odd or negative.

The harmonic function $V_m(0)$ vanishes on $z = \pm h$ so that the function defined by the series

$$V = \sum_{m=0}^{\infty} \frac{C_m}{m!} V_m(0) \tag{3}$$

will be harmonic and will vanish on $z = \pm h$ if the constants $C_m$ are so chosen that (3) is uniformly convergent.

On the surface of the ellipsoid $r = \text{const.}$ (say $\beta$), $V$ must reduce to a constant (say unity). Substituting $r = \beta$ in the right member of (3), setting $V = 1$ and equating coefficients of the Legendre polynomials on both sides of (3) leads to an infinite system of linear equations in infinitely many unknowns $C_m$. This system is of the form

$$(P + Q)\xi = \delta \tag{4}$$

where $P$ and $Q$ are infinite matrices whose elements are respectively functions of $\beta$ and $h$, $\xi$ is a vector $(C_0, C_1, C_2, \ldots)$ and $\delta$ is the vector $(1, 0, 0, 0, \ldots)$. The system (4) is treated by a scheme of successive approximations.

The solution of the problem for the case of an oblate spheroid is entirely similar to that sketched above, and it is merely necessary to replace (1) by the equations of transformation from Cartesian to oblate spheroidal coördinates.

It can be shown readily that the capacity of the ellipsoid lying midway between the two parallel earthed planes is equal to $\epsilon C_0$, where $\epsilon$ is the dielectric constant of the medium in which the ellipsoid is imbedded and $C_0$ is the coefficient of $V_0$ in the expansion (3).

A detailed version of this paper, containing some calculations, is to appear in the *Journal of Terrestrial Magnetism and Atmospheric Electricity*.

[1] Presented to the Am. Math. Soc., Chicago, April, 1934.

[2] Rigby, C. M., *Proc. Lond. Math. Soc.*, **33**, 525–536 (1932).

# THREE THEOREMS ON THE ENVELOPE OF EXTREMALS

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We are concerned with the envelope in the small, more specifically with the conjugate locus in the small. In the large, noteworthy papers have recently been written by Whitehead[4] and Myers,[3] and the reader may also refer to the work of the author.[6]

In the analytic case in the plane, the theory is relatively complete. For a brief account and references see Bolza,[1] pp. 357–369. In 3-space Mason and Bliss[2] have treated the envelope in the case where the envelope is ordinary. Hahn[5] has reduced the minimum problem in 3-space in the non-parametric form to the study of an analytic function of two variables whose Hessian vanishes at the point in question. This transformation of the problem does not, however, clear up the difficulties inherent in the envelope theory.

We shall present three theorems on the envelope which go considerably further than the above theory. Of these theorems the first is a topological characterization of a conjugate point, and has been proved by Morse and Littauer.[7] It will be stated here for completeness. The second theorem is a basic result on the analytic representation of the envelope neighboring one of its points. It is an immediate consequence of two theorems proved by the author, one[9] on the order of a conjugate point, and the other, Morse,[6] p. 235, on the continuation of conjugate points. It is similar to a theorem independently derived from the author's results by Whitehead,[4] p. 690.

The two preceding theorems refer to the analytic case. The final theorem is not so restricted. It gives sufficient conditions for a proper, relative minimum in the problem in parametric form when the end-points $A$ and $B$ of the given extremal $g$ are conjugate. The new conditions are in terms of the position of the envelope without explicit restrictions on the analytic form.

We are concerned with the problem in parametric form with integrand $F(x, \dot{x})$ of class $C'''$ for $(x) = (x_1, \ldots, x_m)$ on an open region $R$ and $(\dot{x}) \neq (0)$. We suppose $F$ is positively homogeneous of order one in $\dot{x}$. Let $g$ be an extremal lying in $R$ with end-points $A$ and $B$. We assume that the Legendre $S$-condition holds along $g$, ref. 6, p. 120. The topological characterization of a conjugate point is as follows. (Morse and Littauer.[7])

THEOREM 1. *If $F$ is analytic, a necessary and sufficient condition that $B$ be a conjugate point of $A$ on $g$ is that the family of extremals issuing from $A$ making sufficiently small angles with $g$ at $A$ shall fail to simply cover the neighborhood of $B$.*

The extremals issuing from $A$ with directions near that of $g$ can be represented in the form (ref. 6, p. 117)

$$x_i = x_i(s, \alpha) \tag{1}$$

where the functions $x_i(s, \alpha)$ are analytic in case $F$ is analytic. Here $s$ represents the arc length along the extremals measured from $A$, and $(\alpha)$ denotes a set of $(m-1)$ parameters $(\alpha)$ taken near the set $(\alpha_0)$ which determines $g$.

The parameters $(\alpha)$ can be chosen so that the Jacobian

$$\Delta(s, \alpha) = \frac{D(x_1, \ldots, x_m)}{D(s, \alpha_1, \ldots, \alpha_n)} \qquad (n = m-1)$$

is not identically zero along $g$. When the parameters are so chosen, the envelope will be defined as the locus of points on the extremals (1) which are determined by the zeros $(s, \alpha)$ of the function $\Delta(s, \alpha)$. Let $s_0$ be the length of $g$. From the result of p. 119 of ref. 6 we infer that $\Delta(s, \alpha_0)$ admits a representation neighboring $(s_0, \alpha_0)$ of the form

$$\Delta(s, \alpha_0) = (s-s_0)^r A(s) \qquad A(s_0) \neq 0$$

in which the integer $r$ is at most $(m-1)$ and $A(s)$ is analytic at $s_0$. The zeros of $\Delta(s, \alpha)$ neighboring $(s_0, \alpha_0)$ will then be zeros of a pseudopolynomial of the form

$$(s-s_0)^r + A_1(\alpha)(s-s_0)^{r-1} + \ldots + A_r(\alpha) = \varphi \tag{2}$$

in which $A_i(\alpha)$ is analytic at $(\alpha_0)$ and vanishes there. The equation $\varphi = 0$ is accordingly satisfied by $r$ roots $s$, real or complex, corresponding to each set $(\alpha)$ sufficiently near $(\alpha_0)$. But according to Lemma 13.3 of Morse,[6] p. 235, these $r$ roots will all be real if $(\alpha)$ is real and sufficiently near $(\alpha_0)$.

The second theorem is then as follows (analytic case):

THEOREM 2. *The sets $(s,\alpha)$ neighboring $(s_0, \alpha_0)$ which determine points on the envelope can be grouped into $r$ real, single-valued, continuous functions*

$$s_i = s_i(\alpha) \qquad (i = 1, \ldots, r)$$

*analytic except at most on analytic loci $M_p$ in the space $(\alpha)$ of dimension $p < m-1$. Any two of these functions which are not identical will be distinct except at most on loci similar to $M_p$.*

We return to the non-analytic case.

Let $A_e$ denote the set of extremals which issue from $A$ and make angles at most $e$ with the ray positively tangent to $g$ at $A$. Let $e'$ and $e''$ be two positive constants and let

$$H(g, e', e'')$$

be the set of points at a distance less than $e'$ from $B$, excluding $B$, and lying

on rays issuing from $B$ making angles less than $e''$ with the ray negatively tangent to $g$ at $B$. With this understood we state the following theorem.

THEOREM 3. *If $B$ is the first conjugate point of $A$, sufficient conditions that $g$ afford a proper strong, relative, minimum in the problem in parametric form are as follows:*

I. *That the Weierstrass and Legendre S-conditions hold along $g$,*

II. *That there exist positive constants $e$, $e'$ and $e''$, such that $H(g, e', e'')$ contains no conjugate point of $A$ on the respective extremals of $A_e$,*

III. *That no extremal of $A_e$ pass through $B$ save $g$.*

In this theorem it is understood that the domain of the points $(x)$ consists of an arbitrarily small neighborhood of $g$.

The proof of this theorem will be published in full.

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## *GROUPS OF ORDER $2^m$ DETERMINED BY SUBGROUPS GENERATED BY THEIR SQUARES*

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If the squares of the operators of a given group $G$ of order $2^m$ generate a cyclic subgroup $H$ of order $2^\alpha$ two cases present themselves. In one of these all the operators of $H$ are invariant under $G$ while in the other these operators are also transformed into their inverses under $G$ since $G$ involves an invariant cyclic subgroup of order $2^{\alpha+1}$ which includes $H$. In the former case the commutator subgroup of $G$ is either the identity

or of order 2 since the quotient group $G/H$ is abelian and of type (1, 1, 1, . . .). It will be convenient to assume in what follows, unless the contrary is stated, that $G$ is not the direct product of two proper subgroups. When it is abelian it must therefore be the cyclic group of order $2^{\alpha+1}$. If we include direct products there is obviously one and only one abelian group of order $2^m$, $m > \alpha$, which has the property that the squares of its operators generate the cyclic group of order $2^\alpha$. When $\alpha = 0$ a group which has the property that the squares of its operators generate the cyclic group of order $2^\alpha$ is necessarily abelian and hence it is included in the theorem which has just been stated. In what follows we assume that $\alpha > 0$.

We shall first consider the case when the commutator subgroup of $G$ is of order 2. Every cyclic subgroup of $G$ whose order exceeds 2 is invariant under $G$ and if every subgroup of order 2 is also invariant $G$ is Hamiltonian and hence its properties are known. It should be noted that $G$ cannot contain more than one invariant subgroup of order 2, because if it contained at least two such subgroups an invariant operator of order 2 in $G$ would not be contained in one of its subgroups of index 2 involving $H$, and hence $G$ would be a direct product. This results from the fact that $G/H$ is abelian and of type (1, 1, 1, . . .) and hence it involves a subgroup of index 2 which excludes an arbitrary operator of order 2 contained in this abelian quotient group. The central of $G$ therefore contains one and only one subgroup of order 2. If $G$ is not Hamiltonian all of its operators which are commutative with one of its non-invariant operators of order 2 constitute a subgroup of index 2 under $G$ whose central is of order 4.

If this subgroup involves a subgroup of order 2 which is non-invariant under it we proceed as before. After $l - 1$ such steps we arrive at a subgroup whose central is of order $2^l$ and which is either abelian or Hamiltonian and involves $H$. In the latter case $\alpha = 1$ since a Hamiltonian group involves no operator of order 8. In the former case the operators of highest order in this abelian subgroup are either of order $2^{\alpha+1}$ or of order $2^\alpha$ as the central of $G$ involves operators of the former order or does not have this property. If it has this property $G$ can be constructed by forming the direct product of the cyclic group of order $2^{\alpha+1}$ and the group of order 2, and then extending this direct product by an operator of order 2 which is commutative with the operators of this cyclic group but transforms the generator of the latter group into itself multiplied by the operator of order 2 contained in the central of $G$. We then form the direct product of the group thus obtained and the group of order 2 and extend it just as before. By continuing this process we finally arrive at $G$.

If the central of $G$ does not involve any operator of order $2^{\alpha+1}$ we can construct $G$ by starting with the cyclic group of order $2^{\alpha+1}$ and extend it by an operator of order 2 which transforms its generators into themselves

multiplied by the invariant operator of order 2 contained in $G$. With this group of order $2^{\alpha+2}$ we then proceed as in the preceding case and continue until we arrive at $G$. Hence there is one and only one group of order $2^{\alpha+\beta}$, $\beta$ being any arbitrary natural number which has the property that the squares of its operators generate a given cyclic group of order $2^{\alpha}$ and that the operators of this cyclic group are invariant under $G$, whenever $\alpha > 1$. Hence there results the following theorem: *Including direct products there are $\beta$ groups of order $2^{\alpha+\beta}$, $\alpha > 1$, which separately have the property that the squares of their operators generate the cyclic group of order $2^{\alpha}$ and that the operators of this cyclic group are invariant under the group.*

When $\alpha = 1$ and the given process of finding successively subgroups composed of the operators which are commutative with a non-invariant operator of order 2 leads to a Hamiltonian group, we can construct $G$ by forming the direct product of the quaternion group and the group of order 2 and then proceeding as before. Hence there is one and only one such group of order $2^{\beta+1}$ whenever $\beta$ is an even number greater than 0. Since the number of groups in this case when we arrive at an abelian group by the given process is the same as when $\alpha > 1$ there results the following theorem: *Including direct products the number of the groups of order $2^{1+\beta}$ which have a subgroup of order 2 as the group of their squares is $3\beta/2$ when $\beta$ is even and $3(\beta-1)/2$ when $\beta$ is odd.*

It remains to consider the case when not all the operators of $H$ are invariant under $G$. Such a $G$ contains also an invariant cyclic subgroup of order $2^{\alpha+1}$ and the operators of this subgroup are transformed under $G$ according to an automorphism of order 2. They are therefore transformed either into their $2^{\alpha}-1$ powers or into their $2^{\alpha+1}-1$ powers under such a $G$ and the operators of $H$ are consequently transformed also into their inverses. This implies that the present case differs only from the one considered above when $\alpha > 1$ and hence it will be assumed in what follows that this condition is satisfied. The operators of $H$ are therefore invariant under a subgroup of index 2 under $G$ which involves all the operators of order $2^{\alpha+1}$ contained in $G$ and is generated by these operators. This subgroup is either one of the groups considered above or it is the direct product of such a group and a group of order 2 since $G$ is still assumed to be no direct product and hence contains only one invariant subgroup of order 2.

When this subgroup of index 2 is of order $2^{\alpha+2l}$ its group of inner isomorphisms is of order $2^{l}$ and it has a set of $2l$ independent generators, each of order $2^{\alpha+1}$. Each of these is transformed in two ways under the additional operators of $G$. Hence these transformations are completely determined and there is one and only one such group of order $2^{\alpha+2l+1}$. On the other hand, when this subgroup is of order $2^{\alpha+2l+1}$ and contains invariant operators of order $2^{\alpha+1}$, these operators can be transformed

either into their inverses or into their $2^\alpha - 1$ powers by the remaining operators of $G$. In the former case there are two such groups while in the latter there is only one. The two groups in the former of these cases can be distinguished by the number of their operators of order 2. This proves the following theorem: *For every value of $\alpha > 1$ and for every value of $l$ there is one and only one group of order $2^{\alpha+2l+1}$ in which the operators of order $2^{\alpha+1}$ generate a subgroup of order $2^{\alpha+2l}$ and there are three and only three groups of order $2^{\alpha+2l+2}$ in which the operators of this order generate a subgroup of order $2^{\alpha+2l+1}$, including invariant operators of order $2^{\alpha+1}$, where $\alpha$ and $l$ have the meanings noted above.*

If the operators of highest order in $G$ generate a subgroup of order $2^{\alpha+2l+1}$ which does not include invariant operators of order $2^{\alpha+1}$, then this subgroup is a direct product and its transformations by the remaining operators of $G$ are completely determined. There is therefore one and only one such group of order $2^{\alpha+2l+2}$. When the operators of order $2^{\alpha+1}$ generate a subgroup of order $2^{\alpha+2l+2}$ this subgroup is again a direct product and its central involves two cyclic subgroups of order $2^{\alpha+1}$. The operators of one of these subgroups are transformed under $G$ into their inverses while those of the other are transformed into their $2^\alpha - 1$ powers. Hence the transformations of this subgroup of index 2 are again completely determined and there is one and only one such group of order $2^{\alpha+2l+3}$. Combining these results with those of the theorem stated at the close of the preceding paragraph, it follows that *there are four groups of order $2^{\alpha+2l+2}$ in which the operators of highest order generate a subgroup of index 2 while there is only one such group of order $2^{\alpha+2l+3}$.*

From the given theorems it results that the groups of order $2^m$ which are not direct products and have the property that their squares in each case generate the cyclic subgroup of order $2^\alpha$, $\alpha > 1$, may be divided into the following four categories: The first of these is composed of those groups in which the operators of highest order generate a group whose central is the cyclic group of order $2^\alpha$. There is one and only one such group for every value of $m > \alpha + 1$. When $m - \alpha$ is even the operator of order $2^\alpha$ which are squares are invariant under this group and when $m - \alpha$ is odd they are transformed also into their inverses. The second category is composed of those groups in which the operators of highest order generate a group whose central is of type $(\alpha, 1)$. Such a group exists only when $m > \alpha + 3$ and there is then one and only one such group when $m - \alpha$ is an arbitrary such even number. The squares of order $2^\alpha$ are transformed also into their inverses under each of these groups.

The third of these categories is composed of those groups in which the operators of highest order generate a group whose central is the cyclic group of order $2^{\alpha+1}$. There is one and only one such group when $m - \alpha$ is an odd number but there are three and only three such groups when

$m - \alpha$ is an arbitrary even number. In the former series of these groups the operators of order $2^\alpha$ which are squares are invariant while in the latter they are transformed also into their inverses. The fourth and last of these categories of groups is composed of those in which the operators of highest order generate a group whose central is of type $(\alpha + 1, 1)$. There is one and only one such group whenever $m - \alpha > 2$ and is odd. The operators of order $2^\alpha$ which are squares are transformed also into their inverses under this group. The direct products of an abelian group of type $(1, 1, 1, \ldots)$ and the groups noted in this and the preceding paragraph constitute all the groups of order $2^m$ which have the property that the squares of their operators generate the cyclic group of order $2^\alpha$, $\alpha > 1$.

The total number of these distinct groups of orders $2^{\alpha+\beta}$, including direct products, is therefore $\beta - 1$ for the first category; $\frac{\beta-2}{2}$ or $\frac{\beta-3}{2}$ for the second category as $\beta$ is even or odd; $2\beta - 1$ or $2\beta$ for the third category as $\beta$ is odd or even; $(\beta - 1)/2$ or $\beta/2 - 1$ for the fourth category as $\beta$ is odd or even. It should be emphasized that in these direct products the centrals of the groups generated by the operators of highest order are not necessarily the same as those noted in the preceding paragraphs. When $\alpha > 1$ the total number of the distinct groups of order $2^{\alpha+\beta}$, including direct products, such that the squares of their operators constitute the cyclic group of order $2^\alpha$ is therefore $4(\beta - 1)$ when $\beta$ is odd and greater than 1. When $\beta = 1$ there is one and only one such group and when $\beta$ is even the number of these groups is $4\beta - 3$. In particular, there are 7, 13, 8, 5, 1 distinct groups of order 64 which have for the groups of the squares of their operators the cyclic subgroups of orders 2, 4, 8, 16, 32, respectively. The total number of these groups is therefore 34.

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## *SEX-MODIFICATION IN THE CHICK EMBRYO RESULTING FROM INJECTIONS OF MALE AND FEMALE HORMONES**

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Since the discovery by Lillie[1] that the free-martin is a female which is modified in the male direction by the action of male sex hormones from a co-twin embryo, investigation has centered on the problem of whether sex-differentiation is more or less controllable or even completely reversible. Experiments were devised for birds and amphibians so as to bring about a relationship between two embryos (parabiosis) or between gonad graft and

host embryo of opposite sexes simulating that found during uterine life between the free-martin and its male mate. Work on the amphibia has brought out the significant point that unlike the unidirectional nature of reversal in heterosexual cattle twins, sex modification may take place in either direction as the result of the action of heterologous sex hormones, and furthermore, the process of inversion may continue until complete (Burns[2]). In the chick, on the contrary, little or no evidence has been obtained for the modification of sex-differentiation by hormone action (see Willier[3,4]).

Although these experiments have contributed to our knowledge of the principles of sex-differentiation the problem still presents many important aspects for investigation. A further analysis is possible now that sex hormones in relatively chemically pure form are available. In using these substances the time of introduction and dosage of hormone may be regulated in a more exact manner than is possible by grafting.

Such experiments were initiated by Kozelka and Gallagher.[5] They discovered that injections of hormone solutions into the hen's egg at an early stage in development bring about the formation in certain embryos of an ovotestis on the left side and a testis on the right. Certain effects on the sex ducts of both sexes were also noted.

The evidence thus obtained for the positive action of hormone solutions led to the present investigation which is conducted on a more extensive scale and scope. Several concentrations of theelin, theelol and bull testis extracts, as well as a variety of extracts of male human urine, were tested. The solvent used for the hormone preparations was also tested for any possible action. In addition normal control embryos from eggs of the same flock of chickens as those used in these experiments were examined for the possible occurrence of atypical structures in the reproductive system. Finally, in one set of experiments the zygotic sex-determination of the embryos is ascertained by means of a sex-linked plumage character (Rhode Island Red ♂ × Barred rock ♀).

A single injection of 0.1 cc. sex-hormone solution (aqueous or in ethylene glycol) of varying potency was made into the albumen of eggs of 24 hours' incubation and development continued until the nineteenth day. Altogether over 350 embryos, including both experimental and normal controls, have been examined macroscopically; the gonads and a portion of one or both Wolffian or Müllerian ducts of 86 of these have been studied histologically.

*Effects of Theelin and Theelol (Dosages Ranging from 0.05 to 2.0 Mg.).*—In the zygotically determined males the right testis, although in general smaller than normal, is usually normal in form (s-shaped cylinder) and histology whereas the left testis (Figs. 1 and 2) has the flattened form of a normal left ovary and consists histologically of both ovarian cortex and testicular tissues (ovotestis). The amount of cortex increases roughly as

the quantity of hormone injected is raised. As this occurs the number of testicular cords decreases correspondingly, being replaced almost completely in many cases and completely in one embryo by medullary cords (♀ form of primary sex cord). In such cases of extreme modification

FIGURE 1

Photomicrograph showing ovotesticular structure of the left gonad of a genetic male embryo which was injected with 0.2 mg. of theelol.

(usually with 1 and 2 mg. doses) the right testis likewise tends to flatten a little and portions of it are found to contain medullary cords. There is no effect upon the Wolffian ducts but the oviducts persist, either partially or completely, and in case the dosage is large enough (i.e., 1 mg. or over) they become hypertrophied (Fig. 2).

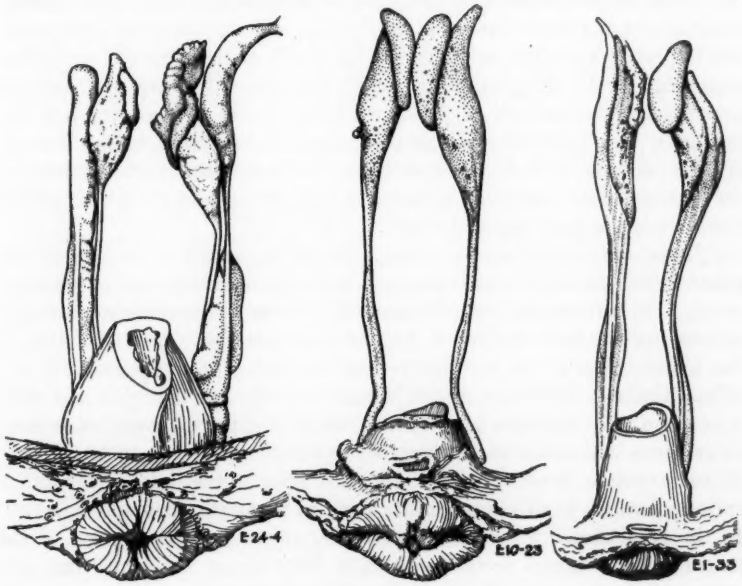
In the zygotically determined females, both right and left ovaries are usually quite normal in size, form and histology regardless of dosage. In a few cases the cortex (typically quite rudimentary or absent in the normal) of the right ovary shows some hypertrophy. There is no effect upon the Wolffian ducts. With low dosage the length of the right oviduct is increased and the left oviduct remains normal or is slightly swollen; with larger dosages both oviducts become much swollen throughout their lengths.

*Effects of Male Hormones.*—Upon injecting male human urine or bull testis extracts in dosages ranging from 9.6 to 200 standard bird units the following results were obtained. *Bull testis hormone* produces no observable effect upon the form, size and histology of the gonads of either sex or upon the oviducts of the females; the Wolffian ducts (potential vasa deferentia) in three out of thirty-three embryos injected with 10 bird units each are slightly swollen (Fig. 3); in one surviving embryo receiving 200 bird units, these ducts are much swollen. *The urine extracts*, regardless of whether the rat vaginal smear test shows the presence or absence of female sex hormone, bring about the formation of a variable amount of cortex on the left testis, in which case the gonad assumes a flattened form. As a rule no change in form, size or structure of the right testis or the ovaries is found irrespective of the dosage; in a few cases more cortex than is typical for the normal has formed on the right ovary. The oviducts are absent in the males as in the normal, whereas in the females their development has been somewhat inhibited since they may be more or less rudimentary or absent altogether. The Wolffian ducts in embryos of both sexes are consistently swollen and frequently to a striking degree (Fig. 4).

*Asymmetrical Differences in Response of the Testes.*—Structural differences in the normal development of the testes account for the differences in their response to the hormones; the left has a stage extending from at least the 7th to the 10th day during which a germinal epithelium is present whereas the right usually has no such structure. This germinal epithelium is shown to be an incipient cortex or cortical rudiment, since upon activation by female hormones it develops into an ovarian cortex. The left testis is, therefore, potentially bisexual whereas the right testis is usually unisexual. Thus for the first time the embryonic testes have been demonstrated to possess the same fundamental asymmetrical difference in bilateral organization that has long been known to be characteristic of left and right ovaries of the domestic fowl. The somewhat rare occurrence of traces of germinal epithelium on the normal right testis leads to the prediction that scattered lumps of cortex might be found equally rarely on the right testis in these experiments. Such has been the case in only four embryos among many injected with female hormones.

On the basis of these findings it is evident that sex hormones do not

originate a morphological component but merely activate one already laid down in normal development. A similar generalization was arrived at by Lillie first for the free-martin[1] and later for the fowl.[6] In the formation of cortex on the testis of the chick we have an example of activation by female hormones in contrast to an apparent suppression of cortex by male hormones in the free-martin gonad.




FIGURES 2, 3 AND 4

Figure 2. Reproductive system of a genetic male embryo treated with 2.0 mg. of theelin. Note flattened ovary-like gonad (ovotestis) on left side (apparent right); right gonad a testis, both oviducts persist and are swollen.

Figure 3. Reproductive system of a genetic male embryo injected with bull-testis extract containing 10 units of male hormone. Both Wolffian ducts show hypertrophy.

Figure 4. Reproductive system of a genetic female embryo injected with male urine extract containing 9.6 units of male hormone. Oviducts absent except for trace of left on lateral surface of Wolffian duct. Wolffian ducts hypertrophied.

*Degree of Intersexuality Produced in Males.*—The degree of sex reversal attained appears to be roughly proportional to the quantity of female hormone injected. With the lower concentrations the gonad formed is intersexual, consisting of both ovarian and testicular tissues; with the highest concentrations used, the original male-determination of the gonad may be largely or even completely overcome so that its structure resembles

closely or is identical with a normal left ovary. When this degree of reversal is attained in the left gonad, the right testis begins to transform into a right ovary as is indicated by the appearance of medullary cords. Oviducts, normally absent in males, persist and with high dosages undergo much hypertrophy.

The primary determining factor in these changes is apparently the activation of the incipient cortex by the female hormones, but whether the transformation of the testicular cords into medullary cords and the persistence and hypertrophy of the oviducts, are the result of the presence of ovarian cortex or due to the positive action of the injected female hormones is somewhat problematical. It is known from studies of ovariotomy in the fowl after hatching that ovarian cortex has an inhibitory influence upon ovarian medulla, so in these experiments the possibility must be admitted that the testicular cords may assume the form of medullary cords under the influence of the superimposed cortex.

*Effective Period of Hormone Action.*—In the formation of the free-martin gonad Lillie[1] has emphasized the importance of the time of onset of hormone action. In heterosexual cattle twins conditions of vascular anastomosis are suitable for the introduction of the male hormones into the circulation of the female twin at or just before the beginning of morphological sex-differentiation. Although in the present experiments the hormones were injected into the albumen prior to the time of origin of the gonad rudiment, no evidence is available as to when they enter the circulation of the embryo. It seems certain, however, that this occurs prior to the onset of sex-differentiation, which begins between the sixth and seventh days of incubation. In the male chick the effective period for response to the action of the female sex hormones probably extends from about the time that sex-differentiation begins until the retrogression of the incipient cortex sets in or, at most, when this process is complete which occurs at approximately the eleventh day.

*Specificity of Action upon Sex Ducts.*—The data show quite clearly that male and female hormones stimulate, respectively, potential male (Wolffian) and female (Müllerian) sex ducts. The specific nature or potency of the sex duct, regardless of the zygotic sex-constitution of the embryo, determines whether or not it responds.

Male hormone from human urine appears to have an inhibiting action upon oviducts of genetic females. This appears to be a result of the direct action of the hormone injected since the ovaries of the same female embryos are apparently unaffected. No inhibiting action of female hormones upon Wolffian ducts has been discerned.

*Differences in Biological Action of the Male Hormone Extracts.*—A distinct biological difference in the action of the male urine extract and the bull testis extract is shown, since the former, even though free from estrogenic

substances, activates the incipient cortex of a testis whereas the latter never has. No such difference in the action of these two products is revealed by the comb growth test. However, chemical differences in the active substances found in these extracts have been noted (Gallagher and Koch[7]). The nature of the difference remains for future elucidation.[8]

* This investigation was aided in part by a grant to the University of Chicago from the Rockefeller Foundation and the NATIONAL RESEARCH COUNCIL and in part by the University of Rochester.

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